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Adaptations and Comparative Anatomy of the Locomotor Apparatus of New World Vultures[1]

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Introduction

The primary purpose of this study is to present the structural differences in the bones and muscles of the locomotor apparatus of the genera of New World vultures (family Cathartidae) and to interpret these in relation to differences in habits. As a corollary, functions of the muscles must be analyzed.

Innervations and the relative positions of nerves, muscles and bones are invaluable in determining the homologies of muscles. Although the discussion of homologies is not a part of this paper, it was felt that any information that would contribute to the subject should be presented for the use of future workers. Accurate homologies of avian muscles can be established only after observing the muscles of many different types.

Another purpose of this research is to save in permanent, available form some record of the anatomy of the California condor, *Gymnogyps californianus*, a species which is nearing extinction. In searching for available material I found not a single complete skeleton, although two were almost complete. The two

1 Contribution from the Museum of Vertebrate Zoology of the University of California.

alcoholic specimens used in this study will furnish as far as is known the only complete skeletons extant. It is important that this condor should not pass unknown into oblivion as have the great auk and the passenger pigeon.

Prior to 1927 most studies of avian anatomy were confined to descriptions of structures with but little emphasis on their functions and adaptations. The monographs of Fürbringer (1888) and Gadow (1891) may be said to be the starting point of most of the subsequent researches in avian myology. Gadow brought up to date all previous studies and attempted to describe all the muscles of the bird, their function, innervation and homology. In many instances the results are still valid, but the scope of his attempt was too great to permit of entirely satisfactory completion. As detailed inquiries of certain bird groups are made, it is necessary to expand and alter our concepts of the musculature, its functions and homologies. Fürbringer limited his study to the upper part of the wing and consequently it is more complete than that of Gadow; but detailed observations again bring out the fact that it is impossible to generalize about an order or a family of birds without studying each genus in it. The muscles and bones and their functions may vary greatly. This may be true even in closely related genera as shown by Burt (1930), Miller (1937), Engels (1940, 1941), and Ashley (1941).

A review of the more important papers dealing with the pelvic musculature has been offered by Hudson (1937). His is the most extensive recent work on the musculature of the hind limb and is significant because of the clear descriptions and comparisons of the muscles of birds of several orders. Unfortunately it was impossible for him to present sufficient details for many kinds of birds. A major omission is the absence of information on innervation.

From the viewpoint of the homology of the avian muscles, the studies of Howell (1936, 1937, 1938) are significant. In these he discusses the innervations and homologies of the hip, thigh, shoulder and upper arm of *Gallus*. No consideration is given however to the more complex problems of the distal muscles of the appendages.

Papers dealing primarily with the anatomy of New World vultures are relatively few if taxonomic studies of fossils are excluded. There have been several studies of the structure of the Falconiformes for the purpose of clarifying questions of taxonomy; among them are those of Beddard (1889), Suschkin (1889, 1900) and Pycraft (1902). The most complete work on the family deals with pterylosis and skull structure: Nitzsch (1867), L. Miller (1937), Compton (1938), A. H. Miller and Fisher (1938), and Fisher (1939, 1941, 1943, 1944, 1945).

Owen (1837) dissected the head of a turkey vulture. Eyton (1849) described the posterior margin of the sternum of the vultures, including some cathartids, and in 1869 published some general descriptions of bones and gave a few measurements. In 1889 Bignon reviewed briefly the air reservoir system of the black vulture. In a series of notes, Beddard (1890, 1902, 1904) reported on the morphology of the heart and trachea of New World vultures and commented upon their relationships.

Engels (1941) was the first to consider the functional aspect of the wing skeleton of the cathartids. In his work on the wing skeleton and flight of hawks some observations were made on *Coragyps* and *Cathartes*.

The relatively few skeletons of any genus that were available to me made impossible the study of differences within a species. This scarcity also prevented the use of a complex statistical treatment. A few skeletons are sufficient, however, to show the major differences with which a study of this type is concerned. The ratios and measurements given in this paper may be significant in the analysis of small differences if used with caution.

Great sexual variation was not found in the series of skeletons of the turkey vulture. Consequently the measurements given are averages of both sexes. Age variation is important in a problem of this nature. Many complications arise. In long-lived birds such as vultures the immature plumage may persist long after the bird assumes adult proportions. Because of the scarcity of skeletal material it was necessary to use some skeletons labeled as immature individuals. However, none was included which was unusually small or which showed ratios out of line with the ratios of known adults.

Muscular development and relative size of individual muscles vary considerably with age and with the activities of the individual. Variation in the habits of adult birds of a single species may cause differences in the development of certain muscles. In the absence of detailed observations of the individual birds before they are collected, one must depend upon average values when comparing the development of their component parts. Small differences must be handled with care or must be disregarded.

Emphasis in this research was on differences, not similarities. Where no differences in structures studied are mentioned, similarity may be assumed. The muscles of *Coragyps* are described in detail and are completely illustrated in the drawings. The bones are described only in so far as necessary to illustrate points of differences. However, many of the structural features of the individual bones may be observed in the photographs.

The nomenclature of the parts of the bones used is that of Howard (1929). The names of the muscles are derived from several sources. Howell (1937, 1938) is the authority for most of the names of the muscles of the shoulder, upper arm, hip and thigh. Shufeldt (1890) is the chief authority for the muscles of the forearm and hand. The names of the muscles of the shank and foot are those of Hudson (1937) who largely followed Gadow (1891). A synonymy of the muscles of the wing is to be found in table 19, of the hind limb in table 42, and of the tail in table 23.

Admittedly some names used are undesirable, but rather than change them on the basis of location and configuration in this one family they are retained. The true homology of muscles cannot be determined from a study of a few genera. Nor should the names of muscles be loosely handled; it is preferable to retain some errors than to introduce new errors.

Method

When possible, the fresh specimens were injected intravenously with an embalming fluid composed of formalin, alcohol, glycerin, carbolic acid and oil of wintergreen and were stored in the same solution. Use of such a mixture prevents the extreme rigidity often encountered in specimens preserved in alcohol or formalin alone.

At the time of dissection complete descriptions of the muscles and the nerves were made, and life-size drawings were laid out by measuring all distances with dial calipers. After completion of the description and the drawing, the muscle was removed as a unit, labeled and preserved in 70 per cent alcohol and glycerin for further comparison and for volumetric study.

The skeletons of *Gallus, Aquila,* and *Pandion* were used for comparative purposes in the study of the hind limb. The chicken represents a generalized type with a walking or a cursorial type of foot that shows no grasping ability. *Pandion* and *Aquila* represent extremes in the development of the predatory grasping foot.

In the analysis of the bony parts of the wing, *Aquila, Buteo, Astur* and *Accipiter* were used for comparison. The accipitrines represent forms demonstrating a strong, swift, flapping flight, while the buteonines both soar and flap.

It is desirable to have two distinct genera or species representing a type used for comparative purposes. Otherwise phylogenetic differences may cover up adaptational modifications. Two forms such as *Astur* and *Accipiter* which have recently been considered congeneric and which show great similarity in their flight patterns may exhibit considerable difference in certain parts of the wing. Thus the modifications as seen in two such forms act as a control on the interpretations of the differences among the cathartids.

Materials

Skeletal material used in this study consisted of two skeletons of *Gymnogyps californianus,* complete except for tail vertebrae, and five incomplete skeletons, four complete skeletons of *Coragyps atratus,* eight of *Cathartes aura,* two of *Vultur gryphus,* two of *Sarcoramphus papa,* six of *Aquila chrysaëtos,* four of *Buteo borealis,* three of *Astur atricapillus,* six of *Accipiter cooperii,* six of *Pandion haliaëtus,* and two complete skeletons of *Gallus domesticus* (one white leghorn and one Rhode Island red).

Alcoholic specimens entirely or partly dissected in the course of this study include: *Gymnogyps californianus* (2), *Vultur gryphus* (1), *Coragyps atratus* (3), *Cathartes aura* (3), *Aquila chrysaëtos* (1), *and Gallus domesticus* (2).

Acknowledgments

It is a pleasure to acknowledge the valuable assistance given by those who furnished a great part of the material vital to this study. The first specimen was obtained from Mr. J. R. Pemberton and Mr. Perry Sprague who found an ailing California condor and on its death shipped it to the Museum of Vertebrate Zoology at Berkeley early in 1937. Dr. W. L. Engels of the University of North Carolina gave me a juvenal black vulture; Mr. E. A. McIlhenny of Avery Island, Louisiana sent eight live black vultures. Mr. Carl Koford, Audubon Research Fellow at the University of California discovered a recently killed California condor in the spring of 1941 and shipped it to Berkeley. Mr. W. Vogt of Lima, Peru, sent an alcoholic specimen of *Vultur gryphus,* and Dr. Loye Miller of the University of California at Los Angeles loaned skeletal material of the Andean condor, the California condor and the royal vulture, *Sarcoramphus papa.*

Koford has allowed me to read over some of his unpublished manuscript on the locomotion of the California condor. McIlhenny has most kindly answered my many questions concerning the black vulture. I also had access to the manuscript of Dr. Victor Coles on the life history of the turkey vulture.

I am especially grateful to Dr. Alden H. Miller, Director of the Museum of Verte-

brate Zoology, for helpful suggestions and criticisms throughout the study. My wife, Mildred L. Fisher, has aided greatly in the preparation of the manuscript and the illustrations.

The Flight of New World Vultures

Many authors have written on bird flight. Unfortunately for this study few have considered the mannerisms of flight exhibited by members of the Cathartidae. Old World vultures have been observed in detail by a number of persons; Hankin (1913, 1923) presents the best general account of their flight. Chamier (1925) has written a detailed account of the mechanics of flight in Old World accipitrids. Recently, Horton-Smith (1938) has attempted a summary of bird flight. In a semi-popular style it is valuable for the general principles of flight, but it offers no specific information on the cathartids.

Marples (1930) has made a study of the wings of birds and the changes during development. The work is important as a basis for interpreting changes and their relation to flight. No vultures were studied. The aeronautics of the flight of gulls have been studied by Brewster (1912) and Bunnell (1930). Averill (1927) and Graham (1932) have made a study of the significance of the emarginated feathers and the alula of the wing.

The papers cited above are only a small part of the voluminous literature on bird flight, but they are the most complete and the most significant on which to base a study of the flight of the vultures found in the Americas.

Koford's manuscript on the flight of the California condor contains the greatest mass of information on flight collected for any cathartid. Consequently, the flight of this condor and the use of its wings will be discussed first; comparisons will then be made with other vultures.

The flight of the California condor is characterized by marked steadiness and stability, by the absence of flapping except in special circumstances and by long straight glider-like traverses extending for several miles.

For all vultures, both cathartid and accipitrid, a definite hour of starting flight has been observed. The hour in southern California is about 8 a.m. in summer for the California condor. The time varies with the age of the bird, wind velocity, temperature and moisture. Koford found that immature condors flap-glided in the same canyon at the same time adults were soaring. This may be the result of lesser supporting surface per unit of body weight in the immature birds; the flight feathers probably are shorter. A fairly strong, steady breeze hastens the hour of beginning flight, but strong gales may hold the birds on their perches or force them down if they are already in the air. Higher temperatures increase heat radiation and hasten flight. Rains may or may not affect the rising time. Light showers preceded and accompanied by cumulus clouds apparently hasten soaring. Heavy rains may force the birds to stay on their perches.

Sunning is a performance which usually precedes the take-off; in the condor, take-offs which are not preceded by this exercise are infrequent and usually are a result of some disturbance. Sunning occurs a few seconds after the sun reaches a bird's perch; occasionally it may take place while the perch is still in shadow. During the process of sunning the wings are fully extended, and the tail is fully

expanded. This posture may be held without change for as long as twelve minutes. One wing may be flexed for preening while the other is still extended, and the bird may turn through 180 degrees without folding its wings.

The take-off for flight varies with the type of perch and the terrain. The condor crouches deliberately for several seconds with wings halfway extended before springing into the air or dropping over the edge of the cliff or off the branch. Examination of a strip of moving picture film of a condor leaving a perch in a dead tree revealed that the legs showed little springing ability. The feet apparently are lifted from the perch by the first flap of the wings. However, the crouch before the take-off indicates that there is at least some springing action by the legs. Frequently the condors hop, using the wings, to a higher perch before taking off. On level ground the condor must run into the wind for a distance varying from twenty-five to forty feet. At the beginning of the run a few hops may be made before breaking into an awkward hopping run or gallop. Sometimes the bird moves with long apparently powerful strides. During the run the body is held horizontally and the neck is extended. Usually the wings are flapped hard about thirty times before the bird actually leaves the ground. In a strong wind a condor is able to take off from the ground or a perch merely by extending the wings while facing the wind.

After the take-off from a perch, soaring may start immediately or the bird may flap a few times. When a bird takes to the air from the ground it may soar at once if the ground has any slope at all. If the ground is level, it flaps two or three times, glides for a similar length of time and then flaps again; this continues until the bird reaches sloping ground or gets enough breeze to soar. However, the maximum number of flaps observed after the take-off is about thirteen. It is significant that the condor ceases flapping at the earliest opportunity. Without exception they proceed downhill as soon as possible.

Once well launched, flapping seldom occurs. Soaring is a stable, steady procedure modified only by small movements of the primaries and alula. The steadiness is well illustrated by the fact that Koford on several occasions has observed a condor scratch its head with its foot without a waver in the vertical and horizontal lines of flight. Changes in the camber of the wing undoubtedly occur, but they cannot be detected in the field. The tips of primaries 3 to 9 are usually separated; the spacing between them is changing constantly.

As suggested by Averill (1927) and Graham (1932) the alula and its attached feathers form a slot or small auxillary plane in front of the main plane of the wing and at an angle to it. The small plane and the slot start the air currents flowing in the right direction before they hit the wing; the relative smallness of the alula decreases the amount of turbulence caused by the main plane, the wing. The double action, of the alula and wing planes, causes the air to flow smoothly over the wing. This in turn allows the anterior edge of the wing to be raised higher to get more lifting power without loss from turbulence above the wing. Separation of the tips of the primaries is increased by their emargination. The separated primaries form wing-slots, and each primary acts as an individual plane. The greater the number of primaries which are separated distally the greater the ease with which the air passes over the wing. Graham (1932:74) states that wing-slotting may increase the lift by two hun-

dred per cent when the anterior edge of the wing forms an angle of forty-two degrees with a horizontal line drawn anteriorly from the posterior edge of the wing.

As a result of the increased angle that is possible with slots, the speed is decreased; but, slower speeds are possible without subsequent stalling if slots are present.

Horton-Smith (1938:150-164) explains in some detail the function of the wing-slots formed by the emargination and separation of the primaries. Experiments in wind tunnels have shown that a broad wing tip may decrease the efficiency as much as fifty per cent. However, if that broad tip is broken up into a number of small tips the efficiency is greatly increased due to a reduction of the "end effect." End effect may be defined as the turbulence caused by air escaping laterally off the wing tips rather than passing off the posterior edge or being moved straight downward. End effect is directly proportional to the width and the length of the plane moving through the air. In the wide-tipped wing the length of the plane equals the length of the wing. In a wing in which the primaries are separated the length of the plane involved is the length to the notch between the primaries.

Another function of wing-slots is in reducing the amount of torsion required of the wing as a whole. As suggested previously, each primary acts as a separate plane. Consequently the individual feathers may be tilted to vary the angle of incidence without movement of the entire wing.

In flex-gliding the alula in the condor is flattened down against the anterior edge of the wing, the hand is partly flexed, and the primaries are approximated. In flex-gliding, speed and not lifting power is desired. Fisher (1902) has shown that the alula is raised, spread and separated from the rest of the wing when pigeons and storks descend for landing. The alula, in the manner suggested above, slows the speed and increases the lifting power to lessen the shock of landing on extended legs. Aymar (1936) shows a series of photographs of *Coragyps, Cathartes, Gymnogyps* and *Vultur* which illustrate the action of the alula and the separated primaries.

In soaring, rapid turns are made either by flapping or by banking in which one wing is depressed and tilted forward. The decreased angle thus produced lessens the lifting power, the wing drops lower and banking is accomplished. Slight turns may be brought about by a clockwise rotation, as observed from the left wing tip, of the manus only. Air currents pushing on the tilted tip of the wing, which now offers a broader under surface at right angles to the wind, tend to retard forward motion on that side. It is probable that most gentle turns are the result of movement of the primaries, either rotation or approximation.

Allen (1887) did not believe that any rotation of the manus was possible because the carpal joint is hinge-like. However, Hankin (1913:191, 213) thought the manus was rotated in the manner described above to act as a means of slowing down that side and causing a turn in direction toward that side. Examination of the skeletons of the cathartids shows that some rotation is possible in the carpal joint. Further, the presence of small muscles whose chief

function seems to be rotation of the hand confirms the theory that rotation occurs.

Flapping in the California condor is slow, laborious and pelicanlike. It is used in taking off from level ground, in flap-gliding, in times of stress, and in landing. In flap-gliding the condor flaps five to seven times and then glides for a similar length of time; the maximum number of flaps ever observed was thirteen. In landing a maximum of five backward flaps has been seen. The infrequency of flapping leads one to believe the condor is not capable of sustaining its weight for any length of time by flapping only. It may be that preferential behavior factors which Engels (1941:66) calls psychobiological factors come into play. However, it is more plausible to think that birds as a rule do what their structure and their instincts force them to do.

The foregoing account of flight in the California condor is by no means complete; only those points have been mentioned that show variation among the New World vultures.

In *Coragyps,* the black vulture, flapping is more frequently observed than in any other genus. McIlhenny (MS) states that black vultures can not take off from level ground without a run. They face the wind and make two or three hops on the ground before springing into the air. He says further that black vultures flap their wings far more than turkey vultures, both when rising and when soaring. Dalgleish (1881:237) observed that "in stormy weather they fly high, beating their wings heavily and not sailing as does their congener, the Turkey buzzard." Evans (1899:140) found that wing action is more labored in the black vulture than in the turkey vulture, and Howell (1924:128) stated that the black vulture is always easily distinguished from *Cathartes* by its habit of alternately flapping and sailing. Knowlton (1902:206) found *Coragyps* not nearly so graceful on the wing as *Cathartes,* "the flight being much heavier and apparently laborious, and is accomplished by considerable flappings of the wings." The broad wing of *Coragyps* is fundamentally a soaring wing, but its shortness decreases its lifting surface. Consequently it resorts to flapping to provide lift and forward movement. The effect of laboriousness of the flight suggested above probably comes from the fact that on many occasions the bird has to flap rather than soar or sail.

Once in the air, the black vulture is almost as stable as *Gymnogyps;* in soaring it does not wobble or deviate from its course as does the turkey vulture. As a rule fewer primaries are visibly separated and movements of the alula are less than in the California condor.

In landing the wings may or may not be flapped backward to function as a brake.

Thus the significant facts about the use of the wing in *Coragyps* are: it flaps more than any other vulture; its take-off from the ground is quicker and is accomplished with a shorter run; in soaring it does not wobble as does *Cathartes;* fewer primaries are separated to act as slots, and movements of the alula are fewer; and, the wings are not always used as a brake in landing.

Use of the wing in *Cathartes* in most respects holds an intermediate position

between *Coragyps* and *Gymnogyps*. It flaps more than does the condor but less than the black vulture. In a strong wind it can take off from level ground merely by extending the wings and facing the wind. In calm weather it soars more easily than any other vulture; as suggested above, the soaring is not steady. The body and wings are continually tilting first to one side and then the other; small gusts of wind throw it off course. However, when on the ground *in calm weather* it has difficulty in rising; it needs a longer run than the black vulture. Flapping flight appears to be more difficult for it than for *Coragyps*. Sprunt (1937) and others have noticed the slow getaway of *Cathartes* as compared to *Coragyps*. On roads in regions where both forms are present it is most frequently the turkey vulture that is hit by automobiles.

Alular movements and the slotting of the primaries is essentially the same as in *Gymnogyps*. The use of the wings as a brake in landing is as in *Coragyps*.

No published accounts of the mannerisms of *Sarcoramphus* are available. No detailed observations on *Vultur* were found; four papers, those of Kofoid (1923), Housse (1940), Adams (1907) and Castellanos (1928) give the impression that the flight in *Vultur* is similar to that in *Gymnogyps*. However, the discussions on flight are brief and for the most part are secondhand accounts.

Osteology of the Wing and Pectoral Girdle

Vultur has the greatest absolute length of wing bones (table 1) of any cathartid, and *Coragyps* has the shortest length. But in relation to body length (table 2) *Cathartes* has the longest and *Coragyps* the shortest wing. If the interacetabular width be added to the body length to give a two-dimensional aspect to body size, we find that *Gymnogyps* has the longest wing and *Coragyps* still has the shortest wing. Summing up wing

TABLE 1.—Average Wing and Leg Lengths, and Ratios Involving Them.

	Wing length	Leg length	Wing: leg	Humerus: femur	Ulna: tibia	Metacarpus: metatarsus	Digit II hand: digit III foot
Accipiter	213	.....	.....	.....	.....	.....	.....
Astur	290	.....	.....	.....	.....	.....	.....
Gallus	.....	350	.....	.....	.....	.....	.....
Pandion	.....	328	.....	.....	.....	.....	.....
Aquila	575	493	117	150	130	98	68.0
Buteo	353	.....	.....	.....	.....	.....	.....
Cathartes	477	334	143	214	150	128	80.5
Coragyps	420	400	105	156	110	91	60.6
Gymnogyps	803	585	137	191	147	115	76.4
Sarcoramphus	532	461	115	169	127	90	95.8
Vultur	867	666	130	183	140	108	75.4

length in relative values, the series from short to long in the cathartids is: *Coragyps*, *Sarcoramphus*, *Vultur*, *Gymnogyps* and *Cathartes*. It is noteworthy that the values for the New World vultures, except *Coragyps*, lie nearer the ratios for *Aquila* and *Buteo* than those for the accipitrine hawks. The figures for *Coragyps* stand almost exactly halfway between the accipitrid and buteonid ratios. Engels (1941:66) found that the wing length in *Coragyps* was comparable to that in the accipitrines.

In relation to leg length, the wing is again shortest in *Coragyps* and longest in *Cathartes* and *Gymnogyps*.

Humerus.—As a part of the functional wing the humerus varies little in length. The ratios of humerus to wing length vary only 2 per cent in the nine genera studied. However, the ratios of humerus to trunk length demonstrate a short humerus in *Accipiter*, *Astur* and *Coragyps*. Humeral lengths in *Sarcoramphus* and *Vultur* fall into the buteonid group while those of *Gymnogyps* and *Cathartes* are much greater. The same indications are apparent in the ratios of humerus to trunk length plus interacetabular width except that *Sarcoramphus* is intermediate to *Astur* and *Buteo*, and *Vultur* seems to approach the value for *Cathartes* and *Gymnogyps*.

TABLE 2.—Ratios Involving the Wing.

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
wing length: trunk length + interacetabular width	207	223	266	263	289	243	302	260	276
wing length: trunk length	254	276	325	325	382	300	370	335	340

Ratios of proportions within the humerus (table 5) reveal the humerus to be stronger in the flapping accipitrine types. In this regard all the cathartids agree closely with the soaring buteonine group. Proximally the humerus is somewhat wider in *Coragyps* and *Sarcoramphus*, which have the same value (20.6) as *Astur* and *Accipiter*. Distally the width is fairly stable, but *Gymnogyps*, *Aquila* and *Buteo* constitute a group with perhaps an insignificantly narrower condylar region. Length of the bicipital crest is greatest in *Coragyps*, *Vultur* and *Sarcoramphus*, but because of the variation in the length of the crest between phylogenetically and functionally similar genera, that is, variation between *Astur* and *Accipiter* and between *Aquila* and *Buteo*, I do not think the differences are important. Because of an inescapable error in determining the distal extent of the deltoid crest, minor variations must be disregarded, but the somewhat longer crest in *Coragyps* may be noted as well as the similarity between the lengths in *Gymnogyps* and *Buteo*.

TABLE 3.—Average Lengths of Wing Bones.*

	Humerus	Radius	Ulna	Metacarpus
Accipiter	71.2 (11)	69.6 (11)	76.5 (11)	39.9 (12)
Astur	96.0 (5)	98.0 (3)	105.6 (3)	51.1 (2)
Aquila	189.8 (11)	209.9 (11)	219.3 (13)	102.9 (13)
Buteo	113.7 (7)	128.8 (8)	134.3 (7)	64.1 (8)
Cathartes	150.0 (15)	169.5 (15)	177.6 (14)	82.8 (16)
Coragyps	134.0 (8)	146.0 (7)	156.0 (8)	75.0 (8)
Gymnogyps	266.0 (8)	293.0 (4)	308.0 (4)	132.0 (3)
Sarcoramphus	169.0 (4)	197.0 (3)	210.0 (2)	89.0 (3)
Vultur	280.0 (4)	326.0 (4)	340.6 (4)	139.5 (4)

Significant differences in the pneumaticity of the humerus are evident. The most striking feature is a large foramen on the palmar surface of the humeral head in *Coragyps*, *Sarcoramphus* and *Gymnogyps*. Scattered over the same surface of the head in *Aquila*, *Vultur*, *Gymnogyps* and *Astur* are a few minute openings. Many may be seen here in *Cathartes*. Only occasionally are they to be found in this part of the humerus in *Buteo*. On the anconal surface (plate 6) there are a few variations in the pneumatic openings. In all nine genera a single large aperture surrounded by several smaller fenestrations in the pneumatic fossa opens into the head and shaft between the

* Numbers in parentheses indicate number of specimens measured.

bicipital and medial crests. In *Coragyps*, *Cathartes*, *Vultur* and *Gymnogyps* there are fairly large openings on the anconal side of the head itself. A few smaller foramina are present here in the other forms. In the brachial depression the largest openings are present in *Coragyps* and *Gymnogyps*, but *Cathartes* and *Sarcoramphus* have a slightly fenestrated depression and a definite aperture anterior and medial to the internal condyle. There are a few small holes in the brachial depression in *Vultur* and *Aquila;* still fewer apertures are present in this region in *Buteo*, *Astur* and *Accipiter*. On the anconal side between the condyles in the humeri of *Cathartes*, *Sarcoramphus* and in some humeri of *Gymnogyps* numerous medium-sized openings are found. Fewer and smaller openings are present in the other genera except in *Accipiter* which has none.

Pneumaticity of the humerus is greater in the cathartids than in the buteonids and accipitrids. Using the size and number of the foramina in the bone as criteria of pneumaticity *Cathartes*, *Gymnogyps* and *Coragyps* have approximately the same degree of pneumaticity; however, the humerus of *Cathartes* may be the most pneumatic. *Sarcoramphus* is intermediate; it has much greater pneumaticity than *Vultur* which is only slightly more pneumatic than *Buteo* and *Aquila*. Of the genera studied, the accipitrines have the least pneumatic bones.

TABLE 4.—Average Lengths of the Digits of the Hand.

	Digit I	Phalanx 1 digit II	Phalanx 2 digit II	Total digit II	Digit III
Accipiter	13.3 (12)	14.4 (12)	10.5 (7)	24.9	6.3 (11)
Astur	18.1 (2)	19.4 (2)	13.7 (2)	33.1	9.0 (2)
Aquila	35.2 (5)	36.4 (12)	26.2 (6)	62.6	17.3 (11)
Buteo	20.7 (8)	23.7 (8)	16.9 (6)	40.6	10.7 (7)
Cathartes	25.5 (15)	35.5 (16)	30.8 (16)	66.3	21.6 (15)
Coragyps	22.7 (7)	29.1 (7)	25.7 (8)	54.8	18.0 (8)
Gymnogyps	40.3 (3)	53.2 (4)	43.9 (4)	97.1	35.0 (4)
Sarcoramphus	31.5 (2)	34.4 (3)	29.2 (3)	63.6	22.0 (3)
Vultur	42.1 (4)	57.2 (4)	50.1 (3)	107.3	38.0 (4)

In *Astur*, *Accipiter*, *Buteo* and *Aquila* the deltoid crest widens sharply halfway down its length so that the proximal half forms a definite angle with the distal half (plate 6). This is most apparent in the first two genera listed. In *Cathartes* and *Coragyps* it widens out more than in the other cathartids in which the crest is narrower and arc-like when viewed from the side. Increased center width of this crest provides better attachments for M. deltoideous major and M. pectoralis superficialis and also provides a greater power arm for their action. The capitular groove is deep in all the forms but somewhat more excavated in the vultures. However, this may be due to increased prominence of the internal tuberosity which like the external tuberosity is better developed in the Cathartidae. The ligamental furrow near the internal tuberosity is more noticeably abrupt and deep in the cathartids.

Distally the humerus bends toward the palmar side at more of an angle in the accipitrines and *Aquila*. *Buteo*, *Coragyps* and *Cathartes* and to a lesser extent *Vultur* approach this condition. *Sarcoramphus* and *Gymnogyps* have slighter bends here. In addition, when viewed from the distal end, the distal end is rotated posteriorly and counterclockwise to a greater degree in the acciptrines and buteonines than in any cathartid, with the possible exception of *Coragyps*. No other important differences in the condylar end of the humerus were noted except that the brachial depression is relatively deeper in the cathartids. The variations in the distal part of the humerus are too small and too inconstant to be of value in differentiating individual bones.

Ulna.—Ratios of ulna to wing length (table 6) indicate that *Astur* and *Accipiter* have a somewhat shorter ulna than do the other genera, but *Coragyps* and *Cathartes* appear to be nearer the accipitrine group than are *Vultur*, *Gymnogyps* and *Sarcoramphus*. *Gymnogyps* has an ulna of about the same relative length as the buteonines, and *Vultur* and *Sarcoramphus* have longer ulnae. This then is the picture of the ulna, but the direction of change is not indicated. If one considers the ratios of ulna to trunk

length and of ulna to trunk plus interacetabular width the direction of modification may be seen. Compared to the ratios for the accipitrids these ratios indicate a definite shortening of the ulna in *Coragyps* and *Sarcoramphus* and perhaps some decrease in length in *Vultur*. However, *Cathartes*, *Gymnogyps* and *Vultur* are in a fairly compact group. In relation to the humeral length the ulna is again shortest in *Coragyps*. The low values for ratio of ulna to humeral length for *Cathartes* and *Gymnogyps* in table 6 are a result of the greater length of the humerus in these forms.

Greater ratios of diameter to length reveal that the shaft is slimmest in *Sarcoramphus*, *Gymnogyps* and *Vultur* with *Coragyps* and *Cathartes* more nearly approximating the accipitrid values. Proximally the width in *Coragyps* and *Cathartes* is about the same as in the accipitrids; other cathartids possess ulnae that are not as heavy as those of the buteonines which in turn are somewhat lighter than those of the accipitrines. With regard to distal width we come to the same conclusions.

TABLE 5.—Ratios Involving the Humerus.

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Length: wing	33.4	33.1	33.0	32.3	31.4	31.9	33.1	31.8	32.3
Length: trunk	84.8	91.4	107.0	105.0	121.0	95.7	122.6	106.0	110.0
Length: trunk length + interacetabular width	69.1	73.8	87.9	85.1	91.0	77.5	100.0	82.4	89.2
Proximal width: length	20.6	20.5	19.8	20.1	18.9	20.6	18.7	20.7	19.3
Distal width: length	18.4	19.1	17.4	17.6	18.1	18.4	17.6	19.4	18.4
Smallest diameter: length	6.7	7.2	6.2	6.1	6.3	6.2	6.0	6.2	5.9
Bicipital crest: length	16.9	17.9	17.7	19.3	17.9	19.0	18.3	19.6	19.3
Deltoid crest: length	31.2	32.2	35.7	34.1	30.2	38.0	33.8	29.0	31.2

One-half to three-fourths of its length distally the ulna bends more toward the palmar side in accipitrines. The buteonines show the next largest bend. In *Coragyps* the bend is more than in *Cathartes* and *Gymnogyps*. In *Sarcoramphus* and *Vultur* the bend is appreciably less than in the other genera and is no greater than the gentle bend found throughout the entire ulnar length in other cathartids. Accompanying this character and exhibited to the same degree by the same genera is a slight bend anteriorly.

In the cathartids the anconal papillae for the secondaries are much more developed than are the more anterior papillae. However, both rows appear more conspicuous here than in the accipitrines and buteonines. The anconal series in cathartids is situated on a definite ridge, more or less absent in the other forms, which constitutes the posterior anconal angle of the ulna. Numbers of anconal papillae for the secondaries usually are: *Gymnogyps*, 15-16; *Vultur*, 17; *Sarcoramphus*, 14; *Cathartes*, 11; *Coragyps*, 8-11. The number of secondaries are: *Gymnogyps*, 22; *Vultur*, 25; *Cathartes*, 18; *Coragyps*, 19; *Sarcoramphus*, 21; (Fisher, 1942:32).

All cathartids possess some pneumatic fenestration of the ulna in the following locations: the impressions for M. brachialis anticus, the internal palmar surface of the internal condyle, the anconal face immediately proximal to the external condyle and the anconal surface of the proximal end between the olecranon and the tricipital attachment. The pneumaticity of the ulna is apparently equally developed in *Cathartes* and *Coragyps*. *Gymnogyps* and *Sarcoramphus* exhibit approximately equal pneumaticity; it is less than in the first two genera. *Vultur*, *Aquila* and *Buteo* form a group showing the characteristics of pneumaticity still less, but in some individuals of *Vultur* there are more foramina than in the other genera.

TABLE 6.—Ratios Involving the Ulna.

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Length: trunk length + interacetabular width	74.3	81.5	101.0	100.0	108.0	90.0	116.0	102.0	109.0
Length: trunk	91.1	101.0	124.0	123.0	144.0	111.4	142.0	132.0	134.0
Length: wing	35.9	36.5	38.1	38.0	37.3	37.1	38.4	39.5	39.3
Length: humerus	107.4	110.0	115.3	117.5	118.7	116.4	115.9	124.3	121.8
Greatest diameter head: length	5.6	5.8	5.0	5.0	5.4	5.5	4.5	4.2	4.3
Proximal width: length	10.9	10.5	10.0	9.8	10.3	10.4	9.7	9.6	9.2
Distal width: length	7.0	7.1	6.3	6.2	6.3	6.5	5.4	5.7	5.5

Radius.—The length of the radius is closely related to the length of the ulna, and no separate analysis of it will be given. As indicated by the data in table 7 the shaft is heaviest in the accipiters, *Coragyps*, *Cathartes* and *Sarcoramphus* and is lightest in *Vultur*, *Gymnogyps* and the buteonids. Proximal and distal widths vary with the strength of the shaft.

Viewed from the anterior anconal position the radius shows two flexures, one toward the posterior in the middle of the shaft and one directed anteriorly between the first and second fourths of the shaft. In *Cathartes* these flexures are developed to their fullest extent; the bending is least apparent in *Vultur*.

The humeral facet of the radius in the buteonines and especially in the accipitrines is much deeper and more ovoid than in the cathartids.

The tendinal groove on the anterior anconal face of the distal end is equally developed in buteonids and cathartids. It is deeper and wider in the accipitrids and perhaps slightly deeper in *Coragyps* than in other cathartids. In the vultures the groove occupies the posterior half of the distal tip of the radius, in accipiters the middle half or the posterior two-thirds of the width of the end, and in buteonines the middle half or the posterior one-third of the surface. The scapholunar articulation is relatively wide and deep in the accipiters and buteos. Because of a greater tendency of the radius to curve posteriorly over the distal end of the ulna in *Astur* and *Accipiter* the ulnar depression is more evident. This curving is also present in *Aquila* and *Buteo* but is less conspicuous. The distal end of the radius in the New World vultures curves only slightly. In birds which flap the wings consistently the better connection between the ulna and radius, represented by the curving over of the radius and by the deeper ulnar facet at

the proximal end, affords less opportunity for dislocation; at the same time there is less opportunity for the movements of the bones upon each other.

Coues (1872) has discussed the possibility of automatic extension and flexion of the hand when the forearm is extended or flexed. He thought that the radius was forced distally on the ulna when the forearm was flexed. Thus the radius pushed on the anterior part of the base of the metacarpus, via the scapholunar bone. This caused the hand to be flexed. In extension of the forearm the converse occurred. The key to this action is the amount of ligamental attachment between the bones; in some forms there is so much

TABLE 7.—Ratios Involving the Radius.

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Greatest diameter of head: length	6.4	6.4	5.4	5.6	6.0	6.2	5.4	5.6	5.5
Greatest shaft diameter: length	3.7	3.5	3.2	3.1	3.6	3.7	3.1	3.4	3.1
Distal width: length	8.1	7.8	7.2	7.1	8.1	8.6	7.3	8.1	7.1

that such a sliding action of the radius is almost certainly precluded. The absence of sharp curving of the radius over the distal end of the ulna and the looser articulations between the bones in cathartids would decrease the efficiency of such an automatic mechanism. This fact plus the greater weight of the manus and its appended remiges in the vultures may in part explain why the wings often droop and are not held up in perfectly flexed position as they are in the accipitrines.

The genera listed in order of decreasing pneumaticity of the radius are: *Coragyps*, *Sarcoramphus*, *Cathartes* and *Gymnogyps*; *Vultur*; *Buteo* and *Aquila*; *Astur* and *Accipiter*.

Metacarpus.—Ratios of metacarpal to wing length in table 8 demonstrate that in accipitrines the metacarpus forms a greater per cent of the wing length than in the other genera. It is of interest that *Coragyps* and *Cathartes* possess values near the figures for the buteonines while the other cathartids show ratios significantly smaller. If, however, the ratios of metacarpus to trunk length and of metacarpus to trunk length plus interacetabular width are studied, it may be observed that the metacarpus is relatively shortest in accipitrines, closely followed by *Coragyps*, *Vultur* and *Sarcoramphus*. In buteonines this bony element is longer than in these cathartids but considerably shorter than in *Gymnogyps* and *Cathartes*. Ratios of metacarpus to humeral length might be thought contradictory to this statement, but the increased humeral lengths in the cathartids, especially *Cathartes* and *Gymnogyps*, more than account for the lower ratios. If the cathartid vultures descended from a type with wing proportions characteristic of a flapping bird it must be assumed that the metacarpus has increased in length the most in *Gymnogyps* and *Cathartes* and the least in *Coragyps*.

Metacarpal II is strongest in *Coragyps*, *Cathartes* and *Gymnogyps*, but it is heavier in all the cathartids than in the other genera; it is slimmest in the buteonines. The intermetacarpal width is somewhat less in the cathartids than in *Aquila* and *Buteo* and is much less than in *Astur* and *Accipiter*. Metacarpal III is heaviest in the vultures. Metacarpal I is larger and has a relatively longer extensor process in accipitrines and buteonines; its anconal surface is more deeply excavated than in cathartids. In accipitrines the facet for the pollex is deeper and smaller in area; therefore the movement of the pollex is more restricted. *Coragyps* possesses more depth in this facet than do the other vultures, but *Buteo* and *Aquila* have the most rounded and the largest facets. Facets for digits II and III in cathartids and buteonids are slightly less convoluted to

fit the proximal ends of their respective phalanges than in the accipitrid genera. In addition, the facets are larger and flatter in the buteonids and cathartids.

The important feature of these facets is that the increased size and flatness allows for flexion and rotation in various directions. Especially is this significant in digit I because of the delicate alular adjustments that are necessary for soaring. Movement of the alula and other bony elements of the manus in soaring birds is easily seen by reason of the consequent motion of the attached flight feathers. It is noteworthy that the various bones of the hand are more loosely articulated in New World vultures. Although *Coragyps* demonstrates the cathartid pattern of length in these bones, the articulations resemble the accipitrid type.

TABLE 8.—Ratios Involving the Metacarpus.

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Length: trunk length + interacetabular width	38.7	42.4	47.7	47.8	50.2	43.4	49.6	43.4	44.6
Length: trunk	47.5	52.5	58.2	58.7	66.8	53.6	60.8	56.0	54.9
Length: wing	18.7	19.0	17.9	18.1	17.4	17.9	16.4	16.7	16.1
Length: humerus	56.0	57.4	54.2	56.1	55.0	56.0	49.6	52.7	50.0
Greatest diameter: length	8.8	8.5	8.3	7.8	10.0	10.0	9.6	9.3	9.1

The process on which the extensor muscles attach on metacarpal I is relatively long in *Astur* and *Accipiter*. It projects proximally to such an extent that its tip is almost flush with the carpal trochlea. In *Buteo* and *Aquila* the attachments are developed as in *Astur*, but they do not extend as far proximally. The process for attachment is shorter and still farther distally in the cathartids. Expressed in per cent of the length of metacarpal II the process for the extensor insertion is situated the following distances from the proximal end of the metacarpus: *Sarcoramphus*, 15 per cent; *Gymnogyps*, 14.3; *Vultur*, 14.1; *Cathartes*, 12.3; *Coragyps*, 10.5; *Aquila*, 8.0; *Buteo*, 7.3; *Astur*, 6.8; and *Accipiter*, 4.5.

Position of this insertion point is of major significance. The well developed, proximal process in *Astur* and *Accipiter* gives increased speed of extension which is necessary in their swift flapping flight used in the pursuit of prey. In *Aquila* and *Buteo* soaring flight predominates, but flapping is more often resorted to than in the cathartids. It is of interest therefore that as regards the position of the extensor insertion on the metacarpus the buteonines are intermediate between the accipitrines and the cathartids. In the New World vultures the distal insertion permits slower but more powerful extension. For sustained extension, as needed by soarers, the distal location eases the work of the extensor muscles. Significant is the more proximal location in *Coragyps;* it indicates perhaps lessened soaring and greater flapping potentialities.

In buteonines and accipitrines the ligamental fossa surrounding the ligamental attachment of the pisiform process is much deeper than in cathartids. *Coragyps* and *Sarcoramphus* exhibit this feature to a greater degree than do the other vultures. The metacarpal elements in *Cathartes* are the most pneumatic. Listed in sequence of decreasing pneumaticity the order is: *Coragyps* and *Gymnogyps*, *Sarcoramphus* and *Vultur*, *Aquila* and *Buteo*, *Astur* and *Accipiter*.

Digit I.—The ratios in table 9 show the pollex to be longer in the buteonines. The vestigial condition of this bone in birds is accompanied by considerable variation in its

length. The differences in the cathartids are of lesser magnitude than those between *Astur* and *Accipiter*. Thus little functional importance may be attached to the variations within the Cathartidae.

The phalanx in the vultures has broader, flatter articulating surfaces and better basally developed muscle insertions.

TABLE 9.—Ratios Involving the Digits of the Hand.

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Digit I: synsacrum length	21.3	23.4	27.3	25.6	21.3	19.6	21.3	22.3	20.1
Phalanx 1, digit II: trunk + interacetabular width	14.0	14.9	16.9	17.7	21.5	16.8	20.0	16.8	18.2
Phalanx 1, digit II: trunk	17.1	18.5	20.6	21.7	28.6	21.0	24.5	21.6	22.4
Phalanx 1, digit II: wing	6.8	6.7	6.3	6.7	7.4	6.9	6.6	6.5	6.6
Phalanx 1, digit II: humerus	20.2	20.2	19.2	20.8	23.7	21.7	20.0	20.4	20.4
Phalanx 2, digit II: trunk	12.5	13.0	14.8	15.5	24.8	18.4	20.2	18.4	19.6
Phalanx 2, digit II: trunk + interacetabular width	10.2	10.5	12.1	12.6	18.7	14.9	16.5	14.2	16.0
Phalanx 2, digit II: wing	4.9	4.7	4.6	4.8	6.5	6.1	5.5	5.5	5.8
Phalanx 2, digit II: humerus	14.7	14.3	13.8	14.8	20.5	19.2	16.5	17.3	17.9
Digit III: synsacrum length	10.0	11.6	13.4	13.2	18.0	15.5	18.5	15.6	18.1

Digit II.—Table 9 reveals interesting modifications in the length of the phalanges of digit II. The ratios of phalanx 1 to wing length indicate few significant facts except that *Cathartes* has perhaps the longest phalanx. But use of the ratios of phalanx 1 to trunk length and of phalanx 1 to trunk length plus interacetabular width enables one to draw conclusions concerning the change in length. Both ratios indicate that *Cathartes* has the longest phalanx 1; *Gymnogyps* has the next longest. Although this phalanx in *Vultur* has lengthened more than in *Coragyps* and *Sarcoramphus*, lengthening has not proceeded as far as in *Cathartes* and *Gymnogyps*. *Aquila* and *Buteo* possess first phalanges of relatively the same length as *Coragyps* and *Sarcoramphus*. Widening has also occurred in the cathartid phalanx, but it is least evident in *Coragyps*.

Phalanx 2 of digit II, when compared to wing length, gives an inaccurate picture of the situation because of changes in the latter length. Ratios of phalanx 2 to trunk length and phalanx 2 to trunk length plus interacetabular width indicate that this phalanx is longest in *Cathartes*. In *Vultur* and *Gymnogyps* no great differences can be seen, but both have a shorter phalanx than *Cathartes*. *Coragyps* and *Sarcoramphus* form a group intermediate to the *Vultur-Gymnogyps* value and the buteonine values. The accipitrids, as is to be expected, again show the shortest phalanx (table 9). Thus digit II is notice-

ably longest in *Cathartes* and shortest in the accipiters. Lengths are significantly less in *Coragyps* and *Sarcoramphus* than those in all other vultures.

Sternum.—Ratios of sternum to trunk length show that, in general, birds such as *Astur* and *Accipiter* have somewhat longer sterna than soaring birds such as *Aquila* and *Buteo*. It is of interest that *Coragyps*, *Cathartes* and *Vultur* are similar in this respect to the soarers, whereas *Gymnogyps*, a bird of slightly less wingspread than *Vultur*, has the relative sternal length of the flapping type. *Sarcoramphus* is intermediate between *Coragyps* and *Gymnogyps*. Although taken at face value, the ratios might indicate greater surface for the attachment of pectoral muscles in the accipitrines, such is not always the case. Because of the great extension of the ventral manubrial spine in these birds the total sternal length is not a true measurement of the area of muscular attachment. *Gymnogyps* and *Sarcoramphus* both have relatively longer sternal muscle origins than do the accipitrines; there is probably little difference among the buteonids, accipitrids, *Coragyps*, *Cathartes*, and *Vultur*. Ratios of sternal to synsacral length indicate that the cathartids have shorter sterna than the flapping types and the buteonids; however, this is probably due in part at least to a shortened synsacrum in the latter which, posterior to the acetabulum, is bent ventrally (plate 10).

To obtain an index of the angle of the two sternal wings or plates, the distance from the bottom of the dorsal sternal trough to a straightedge laid between the last intercostal space on each side was measured. This measurement, the depth of the dorsal trough, was used in two ratios—depth to width between the last intercostal spaces and depth to sternal length. These ratios show the depth to be greatest in the accipitrines and least in *Cathartes* and *Coragyps;* the other genera form an intermediate group. However, the depth in *Aquila* and *Buteo* is slightly more than in the vultures. From these facts it appears that greater depth of the trough is correlated with greater use of the flapping mode of flight. I am unable to discover any reason for the lesser depth in *Cathartes* and *Coragyps* which flap more than the other vultures.

Ratios of anterior width to sternal length indicate the greatest width in *Cathartes* and the butenoids; the other cathartid genera constitute a group with the anterior ends slightly narrower. Accipitrids have both the anterior and posterior ends relatively narrowest, but here again the length of the sternum has been unduly increased in my measurement by the slim, well developed ventral spine. Posterior widths show greater variation, partly due perhaps to the warping of the thin posterolateral corners. In a general way however they demonstrate more width posteriorly in the cathartids (except *Sarcoramphus*) and the buteonines than in the accipitrines.

It is not surprising that the general proportions of the sternum do not vary significantly within a family as small as the Cathartidae. The bone, except for the keel and the articulations with other bones, is well isolated from most external factors which might influence its structure. As a result phylogenetic characters cover up the smaller adaptive modifications.

The keel or carina presents many interesting modifications in the genera studied. In the accipitrines the entire keel is placed farther anterior on the sternum. The buteonid keel takes an intermediate position; in the cathartids the keel is placed the most posteriorly and usually extends to the tip of the xiphial area. No cathartid keel extends its ventral border anteriorly to a position beneath the ventral manubrial spine (plates 3 and 4).

Keel length is greatest in *Astur* and *Accipiter* and shortest in *Aquila* and *Buteo* as demonstrated by the ratios of keel to sternal length. There is only slight variation among the vultures, but it is perhaps shorter in *Vultur*. In relation to keel and sternal lengths the height of the keel is greatest in the accipitrids and *Cathartes*. *Coragyps*, *Sarcoramphus* and *Buteo* possess carinae of greater relative height than do the remaining genera. *Gymnogyps* and *Vultur* have the lowest carinae (table 11). The point at which the keel is highest is variable. In *Cathartes*, *Astur*, *Accipiter*, *Buteo* and *Aquila* this point is at the anterior end; in the other cathartid genera the keel is of a more uniform height and attains its maximum in the middle of its length. Functionally the height of the keel and the area of maximum height are important. Increased height provides for increased development of M. pectoralis superficialis and a bony place for its origin. At the same

time by allowing the muscle origin to extend farther ventrally it increases the efficiency of the muscle by placing the fibers at more of a right angle to the wing. Increased height at the anterior end permits a thickening of the muscle in this region. This increased development of the anterior part of the breast muscles produces a stronger anteriorly directed pull in place of the straight downward depression of the wing. The movement anteriorly at the start of the down stroke of the wing has been shown by Taber (1932a, 1932b) to be of importance in increasing the lifting power of the wing. In this study increased height of the keel and displacement of the keel anteriorly have been found in the accipitrids, and to a lesser extent in the buteonids, which are swift efficient flappers. A low keel, with the height uniformly distributed and reaching its maximum in the middle of its length has been found in *Gymnogyps* and *Vultur* which are slow and laborious flappers.

TABLE 10.—Average Measurements of Sternum.*

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Total length	58.6(6)	78.1(3)	119.8(7)	70.2(4)	79.9(7)	91.0(4)	156.0(4)	112.0(2)	169.5(2)
Anterior width	23.7(6)	34.4(3)	64.1(6)	37.0(4)	43.9(8)	44.9(4)	74.4(3)	53.7(2)	82.7(2)
Posterior width	28.4(6)	44.1(3)	75.6(7)	45.5(2)	54.7(7)	56.5(4)	81.3(4)	56.1(2)	91.7(2)
Keel length	54.6(6)	69.1(3)	89.7(7)	55.8(4)	70.4(7)	80.3(4)	134.5(4)	96.5(2)	135.9(2)
Keel height	16.2(6)	21.6(3)	24.8(7)	16.7(4)	21.4(8)	22.3(4)	33.3(4)	26.2(2)	35.2(2)
Width between last intercostals	24.3(6)	37.7(3)	70.5(6)	41.1(3)	44.2(7)	47.3(4)	70.6(4)	50.7(2)	78.1(2)
Depth of dorsal trough	12.6(6)	17.7(3)	28.2(6)	16.5(3)	14.2(7)	16.9(4)	29.3(4)	20.3(2)	34.0(2)

Thickening of the keel is more pronounced in the Cathartidae, although the buteonine keel is relatively heavier than that of the accipitrines; the ventral border is especially wide in the cathartids. Correlated with the habit of placing the carina on the perch when resting, there are great extensions in width in the second and third quarters of the ventral border of the carina in all the cathartids except *Cathartes* (plates 1 and 2). Why they are absent in this bird I do not know; perhaps the turkey vulture does not so frequently ease the strain on the legs by resting its body weight on the keel. Field observations are deficient as regards this habit.

Eyton (1849), Shufeldt (1883) and Lucas (1889) have all pointed out the great individual variability in the extent of the fenestration of the xiphoidal end of the sternal plate. In the Cathartidae as a family there is much generic variation (plates 1-4), but it is possible to make some general observations. In *Cathartes* the individual differences in fenestration are manifold. *Coragyps* shows no such diversity; the four sterna available are alike in this respect. All the sterna of *Gymnogyps* are similar. *Vultur* and *Sarcoramphus* show more variation than *Coragyps* and *Gymnogyps* but considerably less than *Cathartes*. Perhaps more specimens of cathartids other than *Cathartes* would prove all cathartids to be as variable individually as *Cathartes*. It is significant that all the sterna of *Buteo*, *Astur* and *Accipiter* I have examined have one opening on each side; it is quite variable in size. In eight sterna of *Aquila* there was never more than one opening

* Numbers in parentheses indicate the number of specimens measured.

TABLE 11.—Ratios Involving the Sternum.

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Length: trunk	69.8	74.3	67.8	64.4	64.5	65.0	72.0	70.4	66.7
Length: synsacrum length	135.0	148.0	132.0	125.0	100.0	109.6	114.0	118.0	112.0
Anterior width: length	40.4	44.1	53.3	52.8	54.9	49.3	47.7	47.9	48.6
Posterior width: length	48.5	56.5	63.0	65.0	68.4	62.0	61.5	50.1	53.9
Keel length: length	93.2	88.5	74.7	79.7	88.0	88.2	86.5	86.1	82.4
Keel height: length	27.6	27.7	20.7	23.9	26.8	24.5	21.3	23.4	20.7
Keel height: keel length	29.7	31.3	27.6	29.9	30.4	27.8	24.7	27.1	25.1
Depth of trough: intercostal width	51.8	46.9	40.0	40.1	32.1	35.7	41.2	40.0	43.6
Depth of trough: length	21.5	22.7	23.5	23.5	17.8	18.6	18.7	18.1	20.0

on a side; one sternum had no openings in this region. It may be that age is a factor in ossifying the edges of the fenestrations, but in four skeletons of *Coragyps* no great variation was found; one of these birds was not over one year of age and another was at least three years old judging from the pterylosis of the head. One of the California condor skeletons was of a young bird.

The best development of the ventral manubrial spine is found in the accipitrids and the poorest in the cathartids; *Aquila* and *Buteo* are intermediate. The coracoidal sulci meet in the midline above the ventral spine in *Astur*, *Accipiter*, *Aquila* and *Buteo*. In the Cathartidae only the dorsal edges of the sulci meet; they are separated by the poorly developed ventral spine. The sulci do not meet at all in *Coragyps* and in one specimen of *Vultur*. The coracoidal sulcus in the accipitrines and buteonines is deep and possesses a definite ventral lip along its entire length that ends medially in the manubrial spine. The cathartid sulcus shows no such extensive ventral lip; at the external end of the sulcus there is a remnant of a lip. Most of the bearing surface is situated in the medial half of the sulcus in the vultures; in the others the bearing surface is more equally distributed over the length of the sulcus, and it lies in a straight, almost horizontal line. Due to the curvature of the articulation in New World vultures, potential sidewise movements of the coracoid are more restricted than in the other forms examined.

In the vultures the region of the pneumatic foramen at the anterior end of the dorsal trough is reenforced by an inflated ridge of bone running anterodorsally toward the manubrium from the bottom of the trough.

The number and relative development of the costal facets furnish material for speculation. Counts for the cathartids indicated much individual variation in number in the several genera, and the maximum number was less than the minimum for *Astur* and *Accipiter*. If the New World vultures may be assumed to have arisen from the accipitrid stock, a smaller number of costal facets and a greater numerical variation in the cathartids would lead one to believe there had been a decrease in number in them. A count was made on all the falconiform skeletons available; the data are presented in table 12. Because of variation between the two sides of a single sternum each side of the sternum is used as a count, that is, there are two counts per sternum. It may be concluded from the material in the table that the aberrant forms, including at least the Cathartidae, have lost and are in the process of losing some anterior costal facets on the sternum.

The sternum of the accipitrines and butecnines, judging from the fenestration, possesses more pneumaticity than does the cathartid sternum. In the former a row of foramina in the anterior half of the dorsal trough leads into the carina; this row is entirely absent in the vultures except for some openings anteriorly in the usual position of the pneumatic foramen. However, the costal processes and intercostal spaces as well as the region of the sternocoracoidal process and sternocoracoidal impression are more pneumatic in the Cathartidae (plates 3 and 4). *Cathartes* appears to be the most highly pneumatic of the vultures; in *Coragyps* and *Gymnogyps* the pneumaticity is the same, but these latter two are more pneumatic than *Sarcoramphus* and *Vultur*. Yet the differences are small. It is hard to account for greater relative weight of the sternum in the cathartids.

TABLE 12.—Variation in the Number of Costal Facets.

	Counts	Number of Facets on One Side		Counts	Number
Ictinia	2	6	Polyborus	9	6
Elanus	7	6	"	3	5
"	1	5	Herpetotheres	2	5
Accipiter	69	7	Pandion	7	6
"	6	6	"	1	7
Astur	35	7	"	1	5
"	1	6	Gymnogyps	6	5
Parabuteo	6	7	Vultur	3	6
Buteo	68	7	"	1	5
Aquila	30	7	Sarcoramphus	2	6
Haliaëetus	8	7	"	2	5
Asturina	4	7	Coragyps	3	6
Circus	36	7	"	5	5
"	4	6	Cathartes	2	6
Falco	27	6	"	10	5
"	31	7	"	4	4
"	5	5			

Coracoid.—Length of the coracoid, as shown by ratios in table 14, is relatively greatest in *Cathartes*, *Gymnogyps* and *Sarcoramphus* and is least in the accipitrines, *Aquila* and *Buteo*. *Coragyps* and *Vultur* have significantly shorter coracoids. Shufeldt (1909:34) states that the black vulture has the longest coracoid; by mere observation of the bones this coracoid does appear longer because it is a slimmer bone with less lateral inflation of the shaft than in the other vultures. The ratios of sternal articulation to coracoidal length are of little value because of the variable extension laterally of the thin sternocoracoidal process. All cathartid and buteonid coracoids are stronger than accipitrid coracoids. In accipiters the shaft is much more rounded than in the others; it is of importance that the shaft in *Sarcoramphus* and especially in *Coragyps* approaches the cylindrical condition found in accipiters.

The furcular articulation is not clearly defined on the anterior face of the coracoid in the cathartids. Careful study of the coracoids, scapulae, furculum and sternum when they were glued into proper position leads me to believe that the furculum does not articulate with the coracoid in the Cathartidae. Proximally the external face of the furculum is excavated for the inflated head of the coracoid, but no articulating surface is present. The figures of plate 5 show the furcular facet present only on *Aquila*, *Buteo*, *Astur* and *Accipiter*. In the vultures the attachment is by ligament only.

Differences in the shape of the sternal facet on the coracoid have already been discussed with the sternum.

The procoracoid in *Coragyps* and *Sarcoramphus* is more distally situated than that in other cathartids; its position is similar to that in the accipitrines and buteonines. No major differences in the development of the procoracoid were noticed in the vultures; however, it is weaker here than in the other forms. The brachial tuberosity is wider and more inflated and the depression between the procoracoid and the tuberosity is deeper in *Coragyps*, *Sarcoramphus* and *Vultur* than in the rest of the New World vultures. In

Gymnogyps the depression is the shallowest, and the brachial tuberosity is the smallest. Accipiters possess the largest brachial tuberosity and the deepest depression; in this respect the buteonines are between the accipitrines and *Coragyps*. Since development of this tuberosity and depression and the procoracoid are directly correlated with the development of flight ligaments and muscles in this region we must infer that in the coracoid *Coragyps* and *Sarcoramphus* show better adaptations for strong flight.

TABLE 13.—Average Measurements of Coracoid.*

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Length	35.2(12)	47.8(8)	77.6(13)	49.0(8)	62.7(16)	65.0(8)	108.0(8)	79.2(4)	114.0(4)
Length sternal articulation	14.0(12)	19.3(8)	37.2(13)	22.4(8)	27.1(16)	25.4(8)	37.5(8)	29.2(4)	49.1(4)
Least width below procoracoid	3.1(12)	4.4(8)	12.0(12)	6.6(8)	8.5(16)	7.0(8)	15.6(9)	10.2(4)	15.7(4)
Anteroposterior thickness below procoracoid	3.0(12)	4.0(8)	7.7(13)	4.3(8)	6.0(16)	5.0(8)	10.9(9)	7.9(4)	11.1(4)
Length glenoid facet	7.6(12)	10.7(8)	19.1(13)	11.8(8)	17.1(16)	16.1(8)	29.7(9)	....	31.1(4)
Width glenoid facet	3.4(12)	4.9(8)	10.0(13)	5.7(8)	7.9(16)	7.8(8)	13.0(8)	....	15.1(4)

Miller (1937:51) and Lambrecht (1931:79-81) have correlated the position of the anterior intermuscular line with the development of Mm. supracoracoideus and coracobrachialis posterior. They concluded that lateral shifting of the line meant increased size in M. supracoracoideus and consequent increase in the power of flight. In the buteonids and cathartids the correlation is confirmed; *Sarcoramphus* has the line the most laterally situated, and *Cathartes* and *Gymnogyps* possess a more medial line. In the other genera the line is intermediate in position. The line is most medial however in the accipitrines! It is possible in birds such as the latter which must rotate the wing quickly in flight that a certain balance between M. supracoracoideus and M. coracobrachialis posterior must

TABLE 14.—Ratios Involving the Coracoid.

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Length: trunk	41.8	45.5	43.8	44.9	50.6	46.4	49.8	49.8	44.7
Length: trunk + interacetabular width	34.2	36.8	35.9	36.6	38.0	37.6	40.6	38.6	36.3
Length sternal articulation: length	39.8	40.4	47.9	45.7	43.2	39.1	34.7	36.9	43.1
Cross section below procoracoid: length	26.4	36.8	119.0	57.9	81.3	53.8	157.0	103.0	153.0

* Numbers in parentheses indicate number of specimens measured.

be maintained and that therefore M. coracobrachialis posterior is better developed. One might expect the M. coracobrachialis to be well developed in soaring birds where delicate tilting of the wing is necessary to make use of various air currents.

The bicipital attachment is weaker, and the glenoid and scapular facets are not as deep in the Cathartidae as in the Accipitridae. *Coragyps* presents a somewhat stronger bicipital attachment and deeper facets than the other vultures. Strong attachments and deep facets go hand in hand with a strong, well-braced pectoral girdle needed to withstand the exigencies of flapping flight.

All cathartids possess pneumatic foramina in the sternocoracoidal impression (plate 5), beneath the anteromedial overhang of the brachial tuberosity and on the lateral edge of the glenoid facet. *Coragyps*, *Vultur* and *Gymnogyps* have foramina on the medial edge of this latter facet. The sternocoracoidal impression in *Coragyps*, *Sarcoramphus* and *Vultur* is more highly fenestrated than in *Gymnogyps* and *Cathartes*. Only one region, that located in the depression just ventral to the brachial tuberosity, is consistently fenestrated in the accipitrines studied; the sternal end is usually free of openings. Listed in order of decreasing pneumaticity of the coracoid the Cathartidae are as follows: *Coragyps* and *Vultur*, *Sarcoramphus*, *Cathartes* and *Gymnogyps*.

Scapula.—Scapular length (as indicated by ratios in table 16) is greatest in accipitrines, but in buteonines it is only slightly less. Values for *Sarcoramphus* and *Coragyps* are significantly greater than for the other cathartids; the scapula in *Cathartes* is importantly short. Differences in proximal width are small, but in *Coragyps* the width is the same as in *Buteo* and more nearly approximates the accipitrine width than does the width in any other vulture. In the middle of its length the scapula is widest in *Aquila* and by far the narrowest in *Vultur*. At the same point the thickness is greatest in *Cathartes* and *Gymnogyps* and is least in the accipitrines. Therefore, the scapula is sturdiest in *Cathartes*, *Gymnogyps* and *Aquila*; *Coragyps*, *Vultur* and *Sarcoramphus* have scapulae that are intermediate in these proportions between the other cathartids and accipitrines. In general, the blade appears much narrower, the outward bowing in the center of the scapula is greater, and there is more of a ventral bend in the distal part of the cathartid scapula.

TABLE 15.—Average Measurements of Scapula.*

	Length	Proximal width	Middle width	Middle thickness
Accipiter	49.5 (12)	9.6 (12)	4.8 (12)	1.1 (12)
Astur	65.3 (5)	14.1 (6)	6.5 (6)	1.5 (6)
Aquila	98.5 (13)	25.2 (13)	11.8 (14)	3.0 (14)
Buteo	62.4 (8)	14.1 (8)	6.6 (8)	1.9 (8)
Cathartes	65.1 (15)	16.5 (15)	7.0 (16)	2.5 (16)
Coragyps	74.4 (8)	16.7 (8)	6.8 (8)	2.2 (8)
Gymnogyps	114.0 (8)	27.8 (9)	10.0 (9)	4.3 (9)
Sarcoramphus	87.8 (3)	21.6 (3)	8.2 (3)	2.7 (2)
Vultur	122.5 (4)	28.9 (4)	9.3 (4)	3.9 (4)

The furcular articulation is longer and more pointed in the Accipitridae. In the cathartids the articulating surface is short and rounded and extends farther posteriorly to produce a larger articulating surface. On the proximal lateral face between the furcular and glenoid facets there is a deeper depression in the vultures. In accipitrids the coracoidal articulation is marked by a definite point of inflation; in cathartids this articular area is flat, and the proximal end of the scapula forms an almost straight line between the anterior ends of the furcular and humeral articulations. The anteroventral corner on which the glenoid facet is situated is prominent in the Cathartidae.

In the accipitrid scapulae examined there was usually a pneumatic foramen present on the medial surface of the proximal end; about 50 per cent of the time there was an

* Numbers in parentheses indicate number of specimens measured.

opening present here in the cathartid genera. However, on the external proximal surface in the vultures, foramina were consistently found in two places: just ventral to the furcular articulation and immediately dorsal to the glenoid facet. In only a few instances were the foramina present in accipitrines and buteonines.

Furculum.—Several features of the furcular articulation have been discussed previously (p. 566). The scapular tuberosity is longer and is inflated laterally to form a rather wide, strong articulation in the vultures. The accipiters show scant swelling of the tuberosity, and most furcula of *Aquila* and *Buteo* exhibit none. Coracoidal facets are well developed in all accipitrines and usually are absent in cathartids. The one constant exception in this family is *Cathartes* in which some sort of a facet usually is present. Occasionally in *Coragyps* and *Sarcoramphus* there may be a flattened area, but this never possesses a true articulating surface of dense bone. It is to be noted that both scapular and coracoidal facets, the latter only moderately strong, are found in *Accipiter* and *Astur;* in *Aquila* and *Buteo* only the coracoidal facet is well developed although the furcula extend posteriorly to the scapulae; in the Cathartidae the scapular articulation alone is present (except in *Cathartes*). Thus there seems to be a correlation between the type of flight and the strength of the furcular attachment.

TABLE 16.—Ratios Involving the Scapula.

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Length: trunk	58.9	62.2	55.6	57.2	52.4	53.1	52.5	55.2	48.2
Proximal width: length	19.4	21.6	25.6	22.6	25.4	22.4	24.4	24.6	23.5
Middle width: length	9.7	10.0	11.9	10.6	10.8	9.1	8.8	9.3	7.6
Middle thickness: length	2.2	2.3	3.0	3.0	3.8	3.0	3.8	3.1	3.2

Another interesting variation is in the direction assumed by the furcular process at the symphysis; it points posteriorly in the Accipitridae and anteriorly in the Cathartidae. The process is narrow and sharply pointed in the accipitrines and buteonines but is widely triangular, smooth and blunt in the cathartids. In the vultures the anterior and internal surfaces are very smooth in contrast to the sharp edges and the prominent symphysial ridge in the others. Perhaps one explanation for the reversed direction of the process and the smoothness is the greater need for support of a food-gorged pouch in the vultures. It may be observed in the field that gorging is often so great at a "kill" that the vultures are unable to fly away. Frequently the stuffing in of food is sufficient to stretch the skin and expose wide areas of the ventral apterium. On the other hand, hawks are seldom if ever too full to fly; the explanation may be that they kill their food and consequently may feed oftener. Then too, they have the ability to carry the food away for leisurely consumption in a safe retreat. The smooth surface of the furcula in vultures is adapted to support the relatively thin crop that might be injured by sharp ridges; the furcular process extends forward beneath this weight to give added support and protection.

Pneumatic foramina on the anterior surface of the vulturine furcula are rare. In only one case, in *Cathartes*, was there an opening in the symphysial region. Almost half of the accipitrid and buteonid furcula examined had an opening here. All the genera exhibited fenestration in the usual position at the proximal ends of the clavicles. However, the Cathartidae show considerably more pneumaticity. Because of the strength needed for the scapular attachment in this group the fenestration takes place anterior to the region of the coracoidal facet. In the Accipitridae it occurs between the scapular and coracoidal articulations.

Correlation of Osteological Modifications in the Wing and Variations in the Mode of Flight

Pneumaticity of the bony structure of birds is a modification designed to produce a strong yet light mechanism for efficiency in flight. Although most bones in the bird possess some degree of pneumaticity, this feature reaches its maximum development in the bones of the wing which are the parts of the body most modified for flight.

Humerus.—*Cathartes, Gymnogyps* and *Coragyps* are most highly pneumatic, *Sarcoramphus* is intermediate, and *Vultur* is least pneumatic. The buteonines show less pneumaticity than the cathartines, but more than do the accipitrines.

Ulna.—Equal pneumaticity in *Cathartes* and *Coragyps;* less in *Gymnogyps* and *Sarcoramphus* and still less in *Vultur, Aquila* and *Buteo;* least in the Accipitridae.

Radius.—Listed in order of decreasing pneumaticity, the genera are: (1) *Coragyps,* (2) *Sarcoramphus, Cathartes* and *Gymnogyps,* (3) *Vultur,* (4) *Buteo* and *Aquila,* (5) *Astur* and *Accipiter.*

Metacarpus.—Greatest in the Cathartidae, except *Vultur* which possesses pneumaticity equal to that in the buteonines. Few foramina are present in this element in the Accipitridae.

This survey shows that the bones of the wing are more pneumatic in the New World vultures than in the other genera studied. Within the family Cathartidae the genera listed in order of decreasing pneumaticity of the entire wing complex are: *Cathartes, Gymnogyps, Coragyps, Sarcoramphus* and *Vultur.* The greater weight of the skeleton in *Vultur* is striking.

In accipitrines and buteonines the pneumaticity of the sternum is more pronounced than in the vultures, but there is some variation within the Cathartidae. *Cathartes* is most pneumatic; *Coragyps* and *Gymnogyps* are intermediate, and *Sarcoramphus* and *Vultur* are least pneumatic.

In order of decreasing pneumaticity of the coracoid the forms are: accipitrines, buteonines, *Coragyps* and *Vultur, Sarcoramphus, Cathartes* and *Gymnogyps.* The scapula is approximately equally fenestrated in the forms studied. The cathartid furculum is the most pneumatic.

Increased pneumaticity in the vultures is an adaptation for better soaring flight. In the flapping accipitrines the pneumaticity is least; in the buteonines which are soarers and flappers it is intermediate. Modifications in pneumaticity are most obvious in the wing, and are less apparent in the sternum and coracoid. As suggested previously, lesser modification in the sternum and coracoid may in itself be an adaptation for better flight of all types. The greater weight present ventrally near the center of gravity may act as a stabilizer. The lighter sternum of *Cathartes* may be one of the factors contributing to its inability to soar steadily without wobbling. Less body weight and greater supporting surface are the chief factors. The cathartids with the greatest soaring ability and the least proclivity for flapping (*Cathartes* and *Gymnogyps*) possess the greatest

pneumaticity in the parts of the skeleton examined. No observations on the flapping ability of *Sarcoramphus* and *Vultur* are available, but *Coragyps* which has a heavier skeleton flaps more than do *Cathartes* and *Gymnogyps*.

In addition to the differences in pneumaticity, other structural features of the bones of the wing and pectoral girdle show significant differences. A few of the more important variations will be reviewed briefly.

The deltoid crest is wider in *Coragyps* and *Cathartes* than in the other vultures; it approaches the condition found in the accipitrines. Greater width here provides a larger area for the attachment of M. deltoideus major on the anconal surface and for M. pectoralis superficialis on the palmer side. It also furnishes a longer power arm. Consequently a wider deltoid crest is an adaptation for better depression, elevation and rotation of the wing. The longer arm for action of M. deltoideus major also makes easier the raising of the anterior edge of the wing to increase the angle of incidence.

The metacarpals are stronger in the New World vultures than in the accipitrines, perhaps as an adaptation providing stronger support for the long primaries. The extensor process on the anterior edge of metacarpal I is shorter in all the cathartids than in the accipitrines and it is more distally situated.

Both the length of the process and its position on the metacarpal are important since speed of extension and power of extension are dependent upon these two factors. A long process situated proximally gives greater power, but less speed, than a short process in the same location. In other words, to produce the same amount of extension at the distal end of the metacarpus the distal end of the long extensor process must move through a wider arc than the distal end of a short process. A more distal process allows of less speed but does provide a longer power arm.

As a result, the more proximally situated process in the accipiters is a factor in the speed of extension, and the longer process gives added power. The short process in *Coragyps* situated more proximally than in other vultures provides the mechanism for speedier action than in the other cathartids, but with less power. *Cathartes* is intermediate in this respect between *Coragyps* and the other cathartid genera. Greater speed is necessary in flapping flight than in soaring flight, but to maintain the manus extended for longer periods in soaring, the longer power arm, as indicated by the more distal extensor process, eases the strain on the muscles in *Gymnogyps, Vultur* and *Sarcoramphus*. It is significant that the buteonines, which soar more than the accipiters and flap more than the vultures, are intermediate between the accipitrines and the New World vultures as regards the length of this process and its situation on the metacarpal.

The wider and shallower facets for the articulation of the digits found in the vultures (except *Coragyps*) provide for more varied movements of the distal parts of the wing; in the accipiters, and in *Coragyps* to a lesser extent, the facets are narrower and deeper, which condition aids in holding the bones in place but restricts movements which are necessary for successful soaring flight.

The keel of the sternum is thicker and stronger in vultures than in the other forms examined. The coracoidal articulation is curved to a greater extent

in the cathartids; this largely eliminates sidewise movements of the coracoid, but it does provide a stronger girdle. Fewer costal facets are found in the cathartids than in the other genera.

Height of the keel is greatest in forms which use flapping flight. Among the vultures *Cathartes* has the highest keel, but in *Coragyps* and *Sarcoramphus* the keels are higher than in *Vultur* and *Gymnogyps*. Increased height provides for greater development of M. pectoralis superficialis by furnishing more bony area for its origin, and by moving the origin farther ventrally it increases the vector of force effective in depressing the wing.

The point along the length of the keel at which the greatest height is attained is also important. In the accipiters the height is greatest at the anterior end. This permits of more development anteriorly of Mm. pectoralis superficialis and supracoracoideus, which changes the effective line of pull so that the wing is also pulled forward when depressed by M. pectoralis superficialis. The efficiency of M. supracoracoideus is increased by the more anterior position because the longitudinal axis of the muscle lies more nearly parallel to the desired line of contraction and waste force exerted on the pulley on the coracoid is decreased. Thus it is significant in the consideration of the ability to flap that in *Cathartes* the greatest height of the keel is situated farther anteriorly than in the other New World vultures in which the greatest height is in the middle of the length of the keel.

Depth of the dorsal trough of the sternum is greatest in flapping forms, but *Coragyps* and *Cathartes* do not possess a deeper trough than the other vultures.

The coracoid is stronger, longer, and more rigidly fixed in soaring birds; it is longest in *Cathartes, Gymnogyps* and *Sarcoramphus*. In *Coragyps* and *Vultur* the bone is nearer the accipitrid length. Among the vultures, *Sarcoramphus* and *Coragyps* possess the most cylindrical shaft; the coracoidal shaft is most cylindrical in the accipiters. Development of the brachial tuberosity and the depression between the tuberosity and the procoracoid, which is correlated with the ability to flap the wings, is best in the accipitrines, but it is better in *Coragyps* and *Sarcoramphus* than in any other cathartid. The bicipital attachment among the vultures is best developed in *Coragyps;* in this genus the facets are deeper, a condition which provides a better-braced pectoral girdle.

The longest scapula is found in the accipitrines; it is longer in *Sarcoramphus* and *Coragyps* than in the other cathartids. The scapula is very short in *Cathartes*. A longer scapula furnishes more area for the origin of muscles holding it parallel to the vertebral column and for muscles extending from it to the humerus. Consequently, since the proportions and structures of the coracoid and scapula in *Coragyps* and *Sarcoramphus* more nearly approximate those of the accipitrines which are capable of swift flapping flight, it is indicated that *Coragyps* and *Sarcoramphus* may flap more easily than can the other vultures.

The intramembral proportions of the wing exhibit modifications correlated with the type of flight. Böker (1927, 1935) has made detailed observations on the bones of the wing of many birds; he has set up certain types of flight pattern and has found a positive relation between the major types of flight and the proportions within the wing. Engels (1941) examined the wing skeleton of hawks

and corroborated and extended the studies of Böker (1927). Earlier (1938) Engels found that differences in the proportion of the lengths of the bones in the wing accompanied functional differences in the flight of three cuculiform genera. Due to the small number of specimens used by Böker (1935) in determining subtypes and transitional stages between the major types discussed by him in 1927, Engels (1941:62) believes ". . . no great reliance can be placed on his later figures (Böker, 1935), . . ." The criticism is well founded. Consequently, in this study of the vultures, for which few skeletons were available, only major differences will be considered.

Engels (1938, 1940) has shown that individual variability of intramembral proportions in coots (*Fulica*) and thrashers (*Toxostoma*) is usually less than three per cent in any one species; that is, the standard deviation is less than three per cent of the mean. In coots he demonstrated that correlation of length of parts is closer intramembrally than intermembrally. Throughout this study the findings of Engels have been considered when an attempt was made to estimate the amount of variation. Three ratios have been designed to show the relative length of the wing. These ratios agree in demonstrating a short wing in *Coragyps* and a similar, though slightly longer, wing in *Sarcoramphus*. The wing in *Vultur* approximates the long-winged *Cathartes* and *Gymnogyps* yet it is intermediate. Although the ratio of wing length to trunk length plus interacetabular width indirectly considers body size, direct comparison of wing length and body weight is more revealing. The ratios of wing length to body weight are: *Coragyps*, 93.3; *Cathartes*, 110.1 and *Gymnogyps* 31.9! Thus when weight is considered, *Cathartes* still has the longest wing (bony part), but *Coragyps* possesses a wing three times as long as the wing of *Gymnogyps*. The ratio of wing length to body weight for *Vultur* probably approximates the ratio for *Gymnogyps*, but no weights are available for *Vultur*.

The picture thus far produced of the relative length of the wing is accurate but confusing. The most variable part of the wing structure, the feathers, has not yet been considered. Measurements were made of total wing spread and of the length of each wing on fresh or alcoholic specimens which could be extended. Unfortunately no measurements are available for *Sarcoramphus*. Length between the tips of the fully extended wings was (in one adult specimen of each): *Gymnogyps* (278 cm.), *Vultur* (300 cm.), *Cathartes* (174 cm.). If these wing lengths be compared to body weights the ratios are *Gymnogyps*, 5.0, and *Cathartes* 18.6; gross comparison between the weight of *Gymnogyps* and a single specimen of *Vultur* indicates that the ratio for *Vultur* would approximate that for the California condor.

Wing length alone is only one factor in the functioning of the wing as an organ for support and propulsion. Width of the wing in the center of the series of secondaries is important, as is the relation of this width to wing length. The width in *Gymnogyps* is 40 cm.; in *Cathartes* it is 31 cm.; in *Sarcoramphus*, 33 cm.; and in *Vultur* 47 cm. The ratio of width to wing length is 38.0 in *Sarcoramphus*, 31.5 in *Gymnogyps*, 29.7 in *Vultur* and 25.8 in *Cathartes*. Thus the wing is broadest in *Sarcoramphus* and is narrowest in *Cathartes*.

Total supporting surface of the tail, wings and body was calculated for *Gymnogyps* and *Cathartes*. In the California condor this area was 12532 square

centimeters, and in the turkey vulture it was 4838 square centimeters. When the weights are compared, we find that the California condor has a supporting surface of 497 square centimeters per pound; in the turkey vulture the ratio is 1125 square centimeters per pound. This one factor alone is enough to account for the instability of the soaring turkey vulture as compared to the California condor.

The ratios of the length of the bony parts to trunk and other lengths, and to body weight prove that: *Cathartes* has an outstandingly long wing, that *Gymnogyps* has a relatively longer wing than *Vultur*, and that *Sarcoramphus* and *Coragyps* have the shortest wings. Of the vultures for which figures are available, *Sarcoramphus* has the broadest wing, *Gymnogyps* and *Vultur* possess a somewhat narrower wing, and *Cathartes* has the narrowest wing. The long broad wings of *Gymnogyps* and *Vultur* together with the greater weight of these forms make for stable soaring, but the take-off from level ground is more difficult, and stronger air currents are necessary for soaring. The great supporting surface and the light weight of *Cathartes* enable this bird to soar in periods of very still weather when the California condor is becalmed.

The differences in ability to soar in the California condor and the turkey vulture are apparently related to the time at which soaring is started in the morning and to the currents necessary for soaring. Koford (MS) has observed the two forms in the same canyon in California; he noted that the turkey vultures started soaring at least twenty minutes earlier in the morning and continued later in the day. The condors needed more wind or a warmer day with rising currents for successful soaring.

The short broad wings of *Coragyps* are better adapted for flapping flight. Engels (1941:64) has already noted the short wing in this genus and has shown that its length is comparable to that in the accipitrines.

Proportions within the wing are variable and are apparently correlated with the mode of flight. Intramembral ratios are used to show the differences in the proportions. However, these do not show the direction of modification; that is, they do not indicate whether a bone has increased or decreased in length. Perhaps the most valuable means of indicating change is to compare a part of the wing with the trunk length which is less modifiable.

As a part of the wing the humerus is of about equal length in the various cathartids. When its length is compared to trunk length, one may separate the genera into three groups: humerus shorter than trunk (accipitrines and *Coragyps*), humerus slightly longer than trunk (buteonines, *Sarcoramphus* and *Vultur*), and humerus about a fifth longer than the trunk (*Gymnogyps* and *Cathartes*). In these last two genera the humeral length has increased the most.

No clear cut separation into groups may be made on the basis of ulnar lengths in relation to total wing length. The differences are less than the three per cent of the standard deviation one may expect in individual variations, but the figures in table 6 may indicate a shorter forearm in the flapping types. Ratios of ulnar length to trunk length indicate a much shorter ulna in the accipitrines. The length in *Coragyps* is significantly less than that in any other vulture, and the lengths in *Sarcoramphus* and *Vultur* are less than those in *Cathartes* and *Gymnogyps*. The difference of ten per cent between the closely similar *Accipiter*

and *Astur* as regards ulnar length forces one to remember that small differences in bone lengths must be handled with care when correlations with behavior are made. The ulna has increased in length in all New World vultures, but this increase is least apparent in *Coragyps* and is most noticeable in *Cathartes* and *Gymnogyps*.

The metacarpus constitutes a somewhat greater percentage of the wing in the accipitrines than in the other genera. However, in relation to trunk length the metacarpus is longest in *Cathartes* and shortest in the Accipitridae and *Coragyps*. The increase in length has been less in *Gymnogyps* than in *Cathartes* (table 8).

Phalanx 1 of digit II makes up a greater part of the wing in *Cathartes* than in any other vulture. There is little significant variation otherwise. When the length of this phalanx is compared to trunk length it may be observed that the phalanx has increased greatly in length in *Cathartes*. In *Gymnogyps* the increase is less, but it is still more than in the other genera. The phalanx is shortest in the accipitrines; *Coragyps*, *Vultur* and *Sarcoramphus* agree closely with the buteonids. Phalanx 2 of digit II shows essentially the same modifications except that it has to a considerable degree increased in length in all the vultures.

Therefore, the long wing of *Cathartes* is a result of lengthening of all parts of the wing, but the lengthening has been accentuated distally, in the metacarpus and phalanges of digit II. In *Gymnogyps* and *Vultur* the long wing has been produced by a more equal increase in the length of each segment. Here again a greater increase has occurred distally, but it is relatively less in these genera. *Coragyps* shows the least lengthening of the parts of the wing. Most of the increase has been in the distal parts of the wing, especially the phalanges. In all ratios except those for the phalanges the values for the black vulture closely approximate those for *Astur* and *Accipiter*.

Muscles of the Wing and Pectoral Girdle

M. TENSOR PATAGII LONGUS

Description.—The thin narrow belly of this muscle, which is one-fourth the length of the humerus, is fused to the anterior edge of M. tensor patagii brevis (fig. 1). Opposite the middle of the length of the deltoid crest a flat narrow tendon is formed which extends along the anterior edge of the propatagium and across the anterior surface of the distal end of the radius as the most superficial and anterior of the tendons. It is wider and thicker across the wrist joint.

At the point of forming the tendon, the wide tendon of M. dermo-tensor patagii is fused to the deep anterior surface of M. tensor patagii longus. In two out of four specimens of *Coragyps* dissected, some fibers of M. tensor patagii longus came from the anterior edge of the superficial layer of M. pectoralis superficialis.

Origin.—Fleshy from the dorsomedial edge of the furculum in the region of the coracoidal articulation. The origin is in common with that of M. tensor patagii brevis but anterior to it (fig. 7).

Insertion.—Tendinous on the anteropalmar surface of the proximal part of the extensor process of metacarpal I (fig. 14). In the region of the wrist the tendon is closely adherent to the skin and fascia.

Innervation.—An anteriorly directed twig from the same branch of N. brachialis longus superior that serves M. tensor patagii brevis goes to the deep side of this muscle.

Action.—The main function is to extend the hand and support the anterior edge of the propatagium. At the same time M. tensor patagii longus flexes the forearm on the humerus.

Comparison.—In *Cathartes* there is no attachment of M. tensor patagii longus to M. tensor patagii brevis. There are no muscular fibers present; the tendon is a direct continuation of M. dermo-tensor patagii and is connected weakly to M. pectoralis superficialis. In the middle of the length of the tendon a branch passes posteriorly toward the elbow; it inserts on the skin in the middle of the propatagium. Although there is some insertion as in *Coragyps* the main tendon inserts on the distopalmar corner of the extensor process. This provides for depression of the manus and for better extension than in *Coragyps*. M. tensor patagii longus in *Cathartes* is capable only of tendinous action, but the entire power of M. dermo-tensor patagii is applied to its tendon.

In *Gymnogyps* part of the origin is as in the black vulture, but there is a larger tendinous origin from the tendon of insertion of the superficial layer of M. pectoralis superficialis. In the middle third of its length the distal tendon is more than one centimeter wide and is definitely elastic. Opposite the elbow a wide translucent band runs posteriorly from the main tendon to fuse with the insertion of M. tensor patagii brevis on the M. extensor metacarpi radialis. The insertion is the same as in *Cathartes*.

The only origin in *Vultur* is tendinous from M. pectoralis superficialis. The main tendon is like that in the California condor, but the band running posteriorly from it is weaker and does not extend to M. tensor patagii brevis; it fans out to insert on the middle of the width of the patagium. The insertion is identical to that in *Cathartes* and *Gymnogyps*.

In *Sarcoramphus* the origin is the same as in *Gymnogyps*, but otherwise the muscle is as in the black vulture.

Because of the fusion of the heads of the tensor muscles, it was impossible to measure the volume of the M. tensor patagii longus; but in all the genera the belly of the muscle is small, if it is present at all. Since M. dermo-tensor patagii inserts on the longus tendon in all except *Gymnogyps*, size of this muscle is important; it is best developed in *Cathartes* and is least developed in *Coragyps* and *Sarcoramphus*. The larger volume of the M. tensor patagii longus in *Cathartes* and *Vultur*, plus the more distal insertion, makes extension of the hand easier.

The elasticity of the tendon in *Gymnogyps* and *Vultur* provides for the support of the anterior edge of the patagium even when the wing is partly flexed as in flex-gliding. The shortness of the belly in all the cathartids precludes the possibility of the tendon being tensed by it when the wing is flexed. Another adaptation to support the patagium is the posteriorly directed band from the main tendon at the level of the elbow; this is best developed in *Gymnogyps* and *Vultur* and is absent in *Coragyps* and *Sarcoramphus*.

Consequently, M. tensor patagii longus is best adapted to extend the hand and support the patagium in *Gymnogyps*. *Vultur* and *Cathartes* are intermediate in this respect, and *Sarcoramphus* and *Coragyps* are the least adapted. However, the proximal insertion in the black vulture and royal vulture gives greater speed and may be an adaptation for better flapping flight.

M. DERMO-TENSOR PATAGII

Description.—This is a flat band of muscle lying between the anterior edges of the two semiseparated sheets of the superficial layer of M. pectoralis superficialis, palmar to the deltoid crest. Only its anterior edge is visible superficially, and it is rather intimately connected to M. pectoralis superficialis (fig. 1).

Origin.—By a wide thin tendon from a narrow line on the anterior face of the furculum palmar to the origins of the Mm. tensor patagii longus and tensor patagii brevis.

Insertion.—By strong flat tendon on the deep anterior surface of the tendon of M. tensor patagii longus near the center of the deltoid crest.

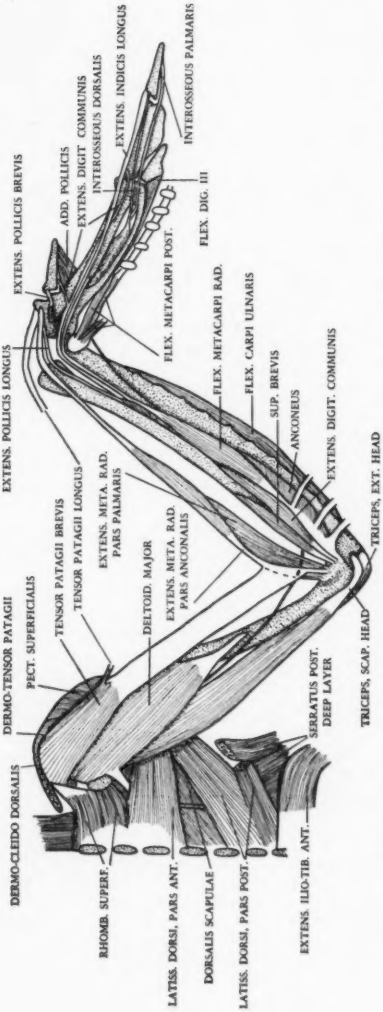


Fig. 1. *Coragyps atratus*. Superficial muscles of the anconal surface of the right shoulder and wing, ×1/3.

Action.—Aids M. tensor patagii longus.

Comparison.—See discussion of M. tensor patagii longus for relative development of this muscle. The configuration is similar in the several vultures, but in *Gymnogyps* the insertion is on the deep anterior edge of M. tensor patagii brevis.

M. TENSOR PATAGII BREVIS

Description.—Anteriorly it covers M. deltoideus major and M. deltoideus minor. The belly is one-third the length of the humerus. The tendon of insertion is wide, thin, and parallel to the anterior edge of the humerus (fig. 1).

Origin.—Fleshy from the superomedial edge of the furculum above the coracoidal articulation and posterior to, but in common with, the origin of M. tensor patagii longus (fig. 7).

Insertion.—By wide, flat tendon on the tendon of origin of the M. extensor metacarpi radialis and on the ectepicondylar prominence of the external humeral condyle in common with the origins of the two parts of M. extensor metacarpi radialis (fig. 10).

Innervation.—A branch of N. brachialis longus superior emerges between M. deltoideus major and M. deltoideus minor and enters the middle of the deep side of the muscle.

Action.—The main action is flexion of the forearm, but because of its insertion on the tendons of M. extensor metacarpi radialis it also is effective in extending the metacarpus.

Comparison.—There is no connection to M. tensor patagii longus in *Cathartes*, and the chief insertion is on the tendon of origin of the anconal fasciculus of M. extensor metacarpi radialis.

In *Gymnogyps* the line of origin is longer, extending anteriorly to cover the articulation between the coracoid and the furculum. In the middle of the deltoid crest the tendon of M. dermo-tensor patagii fuses to the deep anterior surface of the tendon. At the distal end of the deltoid crest three round tendons are formed on the deep side of the broad tendon of insertion; they are intimately attached to the wide tendon. The most anterior tendon inserts strongly on the tendon of origin of M. extensor metacarpi radialis; the middle tendon inserts widely on the broad aponeurosis covering Mm. supinator brevis, extensor digitorum longus and anconeus. The posterior tendon inserts on the ectepicondylar prominence of the external condyle of the humerus.

In both *Gymnogyps* and *Vultur* the wide superficial tendon is closely adherent to the patagium overlying it, and is dissected out with difficulty. It fans out on the forearm to insert broadly on the strong fascia overlying the proximal third of the forearm and extending proximally on to the external humeral condyle.

In *Vultur* the insertion is the same as in *Gymnogyps*.

In *Sarcoramphus* the muscle is similar to that in *Coragyps*.

The muscle is best developed in *Coragyps* and *Cathartes;* it is weakest in *Gymnogyps* (table 18). The more proximal insertion in *Coragyps* and *Sarcoramphus* provides for more speed, but the distal insertion in the other three genera provides a longer power arm to assist the smaller muscles. However, considering both the insertion and the power of the muscle, *Coragyps*, *Sarcoramphus* and *Cathartes* are better able to flex the forearm with it than are *Vultur* and *Gymnogyps*. This is perhaps correlated with the greater ability to flap.

The close attachment of the broad superficial tendon to the patagium in the condors is significant. It aids in tensing the propatagium when the wing is partly flexed. Since the anterior edge of the patagium is one of the chief factors in controlling the camber and angle of the plane of the wing, greater control of the patagium, as possessed by *Gymnogyps* and *Vultur*, is an adaptation increasing their soaring and gliding potentialities.

M. PECTORALIS SUPERFICIALIS

The muscle is in two distinct layers; these will be considered separately. Gadow (1890:243) mentioned two layers in a few birds. Fürbringer (1888:432) noted the two layers in *Catharista atrata*.

Description. Superficial layer.—It lies superficially on the breast and completely covers the deep layer of M. pectoralis superficialis. It extends dorsally on the side of the body to cover the ventral third of the length of true ribs 3 and 4. The anterolateral edge of the muscle divides into two layers; M. dermo-tensor patagii lies between the layers.

Deep layer.—The fibers in this muscle are shorter than in the superficial layer, and the muscle is much smaller. It is entirely covered by the superficial layer, and it covers all except the posterior tip of M. supracoracoideus (fig. 5). Laterally the muscle forms a tendon which extends from the furculum to the distal end of the deltoid crest. The posterior part of the muscle forms a tendon in the region ventral to the fleshy head of the biceps. Blood vessels to the superficial layer perforate the posterior edge of the deep layer.

Origin.—Superficial layer.—Most of the origin is fleshy from the ventrolateral surface of the sternum, from the ventral part of the lateral surface of the keel and from the ventrolateral edge of the furculum from the coracoidal articulation medially almost to the midline of the body (fig. 8). The most anterior and lateral part from the furculum is partly tendinous. The origin does not extend dorsally on to the ribs.

Deep layer.—The origin is fleshy from the keel and from the lateral aspect of the furculum deep to the origin of the superficial layer (fig. 8). The distal half of the origin from the furculum is approximately one-half tendinous.

Insertion.—Superficial layer.—On the palmar surface of the deltoid crest (fig. 10). The anterior third of this insertion is on a narrow line by an aponeurosis; the distal two-thirds is fleshy from a wide area.

Deep layer.—The inserting tendon is superficial to and intimately connected to the long head of the biceps; it attaches to a tubercle on the palmar surface of the humerus at the distal end of the deltoid crest (fig. 10).

Innervation. Superficial layer.—A large branch of N. brachialis longus inferior enters the deep surface in the middle of the muscle. This nerve branch is the second most proximal branch; the most proximal branch is to the M. coracobrachialis posterior.

Deep layer.—A more anterior twig of the branch to the superficial layer passes out dorsal and lateral to M. coracobrachialis posterior and enters the deep side of the middle of the belly.

Action. Superficial layer.—Depresses the wing as a whole and depresses the anterior edge of the wing. This double action is especially important in flapping flight. As the wing starts on the downstroke the anterior edge is depressed. If the wing were held horizontally and depressed, air would escape past both edges, resulting in turbulence in front of the wings; the only possible force would be vertically upward. By depressing the anterior edge the air mass is cleanly divided, and no air escapes past the anterior edge. Further, a forward motion is imparted to the body as the wing is pulled posteriorly in the later phases of the downstroke.

Deep layer.—Aids the superficial layer in depressing the wing. Because of its insertion on the shaft, rather than the deltoid crest, of the humerus, the force effective in depressing the anterior edge of the wing is less. The more anterior position of the origin of the deep layer, as compared to the major part of the superficial layer, increases the ability to move the wing anteriorly. Immediately prior to the beginning of the downstroke and during the early part of the depression the wing is moved forward. It is possible for this deep layer to be a factor in the forward motion; synergistic action by M. deltoideus major and M. supracoracoideus could for example counteract the downward component of force exerted by the deep layer, leaving only the forward force effective.

When a bird is gaining altitude the wings are brought forward to raise the anterior end of the body and increase the angle of incidence. This shifting of the wings forward and backward changes the relation between the center of gravity and the supporting area, the wings.

Comparison. Superficial layer.—In *Cathartes* the origin is entirely fleshy, and there is no origin from the medial half of the furculum. The origin covers the external face of the distal half of this bone ventral to the coracoid.

In *Gymnogyps* this layer completely covers all other breast muscles, and the posterior part of the muscle is by far the best developed. The origin from the carina is on a narrow tendinous line; it becomes fleshy posterior to the origin of the deep layer. From the sternal plate the origin is the same as in *Coragyps* except that it does not include the posterolateral tip of the plate. The superficial layer also originates fleshily from the sternal parts of true ribs 4, 5 and 6 and from the membranes between them; this is an extensive area of origin.

The layer in *Vultur* is similar to that in *Gymnogyps*, but takes fleshy origin from the posterior third of the keel. The middle one-third of the muscle overlying the fleshy part of the deep layer is entirely tendinous.

There is little origin from the ribs in *Sarcoramphus*, but some fibers arise from the body musculature over the ribs. The origin does not extend laterally to cover the posterolateral process of the sternal plate; from the furculum the origin is tendinous and is limited to the medial two-thirds of the furcular length. The insertion is limited to the distal two-thirds of the deltoid crest.

Deep layer.—In all cathartids, except *Coragyps*, there is no tendinous origin from the distal half of the furculum or coracoid. The absence of the strong anterodorsal part decreases the ability to pull the wing forward.

The ratios of the volume of the superficial layer of M. pectoralis superficialis to the volume of the wing musculature (table 18) indicate that it is best developed in *Cathartes*, slightly weaker in *Sarcoramphus*, equally developed in *Coragyps* and *Vultur* and least developed in *Gymnogyps*. These ratios however do not portray the entire situation; differences in body weight and wing length are not considered. If the ratios of volume to wing length are calculated the result is: *Cathartes*, 26.4; *Coragyps*, 17.9; *Sarcoramphus*, 39.1; *Gymnogyps*, 60.9; *Vultur*, 62.3. Ratios of the volume of the superficial layer to body weight are: *Cathartes*, 29.3; *Coragyps*, 16.6; *Gymnogyps*, 11.3; *Vultur*, 18.0?; *Sarcoramphus*, 25.1? (no weight available on specimens dissected). *Cathartes* has the strongest M. pectoralis superficialis, and *Gymnogyps* possesses the weakest muscle. In *Vultur* and *Sarcoramphus* it is almost as well developed as in *Cathartes*, but in *Coragyps* the muscle is only slightly larger than in *Gymnogyps*. The small size of the muscle is a major factor in the laboriousness of flapping flight in the black vultures and the California condor, and the chief reason *Coragyps* flaps more than *Gymnogyps* and *Cathartes* is that it lacks the ability to soar as successfully.

The deep layer is largest in *Gymnogyps* and *Vultur* and is smallest in *Coragyps*. As was the case in the superficial layer however, the muscle is most advantageously placed in the black vulture. This probably offsets the difference in volume between *Cathartes* and *Coragyps* to produce the more effective muscle in the black vulture. The posterior location of the deep layer in *Gymnogyps* and *Vultur* is a disadvantage; the greater size of the muscle in these birds is probably a compensatory modification.

Another factor in the lesser ability of *Vultur* and *Gymnogyps* for flapping is the absence of a strong fleshy anterior part of the superficial layer.

M. SUPRACORACOIDEUS

Description.—Anteriorly it covers the sternocoracoidal articulation and is in contact laterally with the M. coracobrachialis posterior. As it passes anterodistally along the ventral surface of the coracoid it narrows gradually and forms a tendon on the deep side only, next to the coracoid, in the middle of the length of the coracoid (fig. 6). This narrowed tendon with the superficial fleshy part passes dorsally distal to the procoracoid, goes through the triosseal canal and then courses distally to its insertion on the humerus.

A separate fasciculus of this muscles is the thin but wide fleshy portion arising from the medial edge of the coracoid and the membrane between the coracoid and furculum. Apparently this is the fasciculus in tubinares which was described as M. pectoralis tertius (M. coracobrachialis posterior) by Forbes (1885:389).

Origin.—Fleshy from a triangular area on the anteromedial part of the sternal plate and extending caudally almost to the end of the sternum (fig. 8). The origin on the keel extends anteriorly on to the ligament connecting the keel and the furculum. A few fibers arise from the medial edge of the proximal end of the coracoid.

Insertion.—The main insertion is by a strong tendon on the anconal surface of the external tuberosity of the humerus. The small anterior fasciculus crosses this tendon to insert tendinously on the proximopalmar surface of the deltoid crest (fig. 10).

Innervation.—A branch from the trunk that farther distally forms N. brachialis longus inferior passes across the ventral face of the coracoid proximal to the procoracoid and enters the middle of the distal third of the muscle.

Action.—The main function is elevation of the humerus, but the anterior fasciculus tends also to flex the humerus anteriorly. The muscle thus raises the wing, although it is situated ventral to the axis of the wing in order to lower the center of gravity of the bird. Such action is possible because the triosseal canal serves as a pulley.

Comparison.—In *Cathartes* the muscle does not extend on to the caudal fifth of the sternal length. The fleshy anterior fasciculus is larger and more anteriorly situated; the longitudinal axis of the muscle more nearly parallels the direction of force serving to raise the humerus.

In *Gymnogyps* and *Cathartes* the muscle is similar, but the origin from the coracoid in *Gymnogyps* is limited to the proximal end of the anterior intermuscular line.

In *Vultur* the muscle is as in *Gymnogyps* except that the anterior fasciculus is larger.

In *Sarcoramphus* there is quite extensive origin from the medial surface of the proximal third of the coracoid.

Ratios in table 18 demonstrate that M. supracoracoideus is best developed in *Vultur* and is only slightly weaker in *Coragyps* and *Sarcoramphus*. In *Gymnogyps* it is stronger than in *Cathartes*. The differences are even larger if the relatively short wing of *Coragyps*, as compared to *Cathartes*, is considered. Greater size of M. supracoracoideus and the consequent better ability to raise the wing are correlated with the greater speed of flapping shown by the black vulture. Large heavy birds usually beat the wings slowly and depend as much on the fall of the body as on active muscular action to raise the wings. Good development of M. supracoracoideus enables the bird to elevate the wings more easily and to continue the action without undue fatigue; consequently it is an adaptation for flapping flight.

M. CORACOBRACHIALIS POSTERIOR

Description.—This relatively short muscle lies along the anterolateral edge of the coracoid. The belly is large, thick and cylindrical and is divided into two semiseparated fasciculi. It is lateral to M. supracoracoideus and at its point of insertion is partly covered by M. subcoracoideus (fig. 5).

Origin.— Fleshy from the ventrolateral surface of the coracoid; a narrow tip extends posteriorly on to the anterolateral corner of the sternum on the sternocoracoidal process (fig. 8).

Insertion.—By a short tendon on the internal tuberosity of the humerus posterior and anconal to the insertion of M. coracobrachialis (fig. 10).

Innervation.—From N. brachialis longus inferior. A branch of this nerve sends a twig into each of the two parts on their deep surfaces.

Action.—Shufeldt (1890:76) states that "this muscle assists the pectoralis secundus in elevating the humerus. . . ." This is impossible! It depresses the wing as a whole and

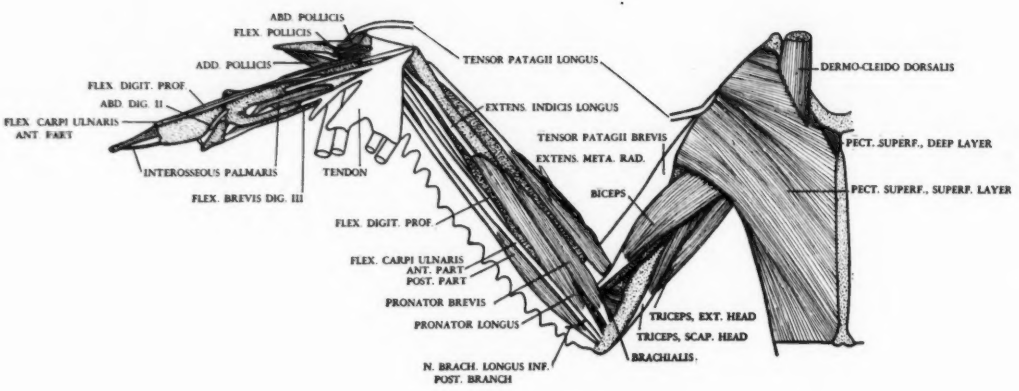


Fig. 2. *Coragyps atratus*. Superficial muscles of the palmar surface of the right wing, ×1/3.

rotates the humerus so as to elevate the anterior edge of the wing. If the humerus is flexed anteriorly, the M. coracobrachialis posterior may assist in pulling it posteriorly.

Comparison.—The muscle is similar in the genera of the New World vultures. Differences in the relative volume are small, but there is some indication that the muscle is smaller in *Sarcoramphus*. Development of the muscle is in part correlated with ability to elevate the anterior edge of the wing which in turn is related to soaring and flapping.

M. LATISSIMUS DORSI

Description.—M. latissimus dorsi consists of two large slips and a dermal component. The anterior part enters the musculature of the upper arm between the scapular and external heads of the triceps. The posterior head passes anterolaterally across M. rhomboideus profundus, the scapula and M. dorsalis scapulae and goes beneath the anterior head as a wide thin tendon. The dermal component overlies the caudal edge of the posterior fasciculus; it is approximately half as long as this part, but is only slightly smaller than the anterior slip (fig. 1).

Origin.—Anterior part.—The origin is mainly tendinous from the dorsolateral corners of the neural crests of the fourth and fifth vertebrae anterior to the synsacrum, immediately dorsal to the origin of M. rhomboideus superficialis.

Posterior part.—Fleshy from the dorsolateral edge of the neural crest of the first vertebra anterior to the pelvis and from the anterior edge of the ilium. The dermal component arises fleshily superficial to the caudal half of the origin of the posterior slip.

Insertion.—Tendinous and fleshy on a longitudinal line in the second fifth of the humeral length between the origin of the external head of M. triceps and the proximal insertion of M. deltoideus major. The posterior head inserts tendinously on the deep side of the anterior head and also sends a thin tendon to the humerus (fig. 10). The dermal component inserts fleshily on the skin beneath the posteromedial corner of the humeral feather tract.

Innervation.—The cutaneous nerve pierces the anterior slip lateral to the fourth vertebra anterior to the pelvis. The posterior part is pierced by a spinal nerve emerging between the anterior edge of the ilium and the transverse process of the first vertebra anterior to the synsacrum; this branch passes to the skin. The muscle is however innervated by a twig of N. brachialis longus superior that passes dorsally to the muscle past the posterior edge of M. dorsalis scapulae. It branches and sends a twig to the deep surfaces of the two parts.

Action.—M. latissimus dorsi pulls the humerus posteriorly and at the same time tends to elevate the anterior edge of the wing; the latter action is weak. Thus this muscle is useful in holding the humerus in a partly flexed condition as in flex-gliding and in moving the entire wing posteriorly in the shifting of the center of gravity forward, in relation to the wings. The dermal component pulls the humeral feather tract medially and is therefore useful in spreading the feathers and in holding them next to the body to prevent the loss of supporting air between the body and the wing.

Comparison.—In *Cathartes* the origin of the anterior part is wider, completely covers the middle slip of M. rhomboideus superficialis and takes origin from vertebrae 4, 5, 6 and 7 anterior to the synsacrum. There is no distinct dermal component, but the posterior part is closely attached to the skin and consequently assumes most of the function of a dermal component.

In *Gymnogyps* there are two dermal slips. A wide thin layer is superficial to the caudal edge of the posterior fasciculus of M. latissimus dorsi. Distally this layer fuses with the two dermal fasciculi of M. serratus posterior and inserts on the posterior end of the humeral tract. As the posterior part passes beneath the anterior part and beneath M. triceps it sends a wide tendon to the deep surface of M. triceps. This tendon is continuous anteriorly with a tendon from the posterior part that inserts immediately posterior to the humeral tendon of origin of the scapular head of M. triceps.

In *Vultur* the muscle is similar to that in *Gymnogyps*, but there is no narrow dermal component as in *Coragyps*.

In *Sarcoramphus* the origin of the posterior part extends on to M. ilio-tibialis anterior.

The muscle is best developed in *Gymnogyps*. It is somewhat smaller in *Coragyps*, *Sarcoramphus* and *Vultur*, and is smallest in *Cathartes*. The larger size in *Gymnogyps* is largely the result of the additional dermal slip, and part at least, of the decreased size in *Cathartes* is due to the absence of a distinct dermal part.

The more anterior situation of the anterior fasciculus in *Cathartes* lessens the efficiency of the muscle by decreasing the vector of force operating to flex the humerus posteriorly. Larger size and a more advantageous situation in *Coragyps* make the muscle most effective for pulling the humerus posteriorly.

The two parts attaching to the humeral tract in *Gymnogyps* give this condor the best ability to flatten and hold down the feathers against the upward force of air and to prevent the escape of air next to the body. *Vultur* with its single wide dermal fasciculus can control the humeral tract better than can *Cathartes* and *Coragyps*.

M. RHOMBOIDEUS SUPERFICIALIS

Description.—This wide but short muscle extends from the second to the seventh vertebra anterior to the synsacrum (fig. 1). In the anterior half the fibers are directed straight laterally, but in the posterior half they pass anterolaterally to the scapula.

Origin.—By extremely thin aponeurosis from the dorsolateral edges of the neural crests of vertebrae 2 to 7 anterior to the synsacrum. The anterior half of this origin is twice as thick as the posterior half.

Insertion.—Fleshy throughout the caudal 1.5 centimeters of the dorsomedial surface of the dorsal end of the furculum, and on the dorsal edge of the anterior three-fourths of the scapula superficial to the insertion of M. rhomboideus profundus (fig. 9). On the dorsal edge of the neck of the scapula the insertion is interrupted by emerging blood vessels.

Innervation.—A nerve trunk formed by spinal nerves of the posterior cervical region emerges from beneath the anterior edge of M. rhomboideus profundus, and a twig enters the middle of the length of muscle opposite the neck of the scapula.

Action.—Raises the scapula and the furculum and moves them medially. Tension in this muscle is important in maintaining the position of the bones when muscles arising from the bones contract to move the humerus. The posterior part of the muscle may aid slightly in moving the shoulder caudally to pull the entire wing backward, as in flex-gliding.

Comparison.—The muscle is similar in the several vultures. In *Vultur* and *Sarcoramphus* the insertion is on the entire dorsal surface of the furculum, and the muscle is stronger anteriorly.

Ratios in table 18 indicate that the muscle is best developed in *Sarcoramphus;* in *Gymnogyps* it is three-fourths as large relatively. It is least developed in *Cathartes* and slightly stronger in *Coragyps* and *Vultur*.

M. RHOMBOIDEUS PROFUNDUS

Description.—Except for the caudal one-fourth, the muscle is deep to M. rhomboideus superficialis. Spinal nerves which pierce the sheet of muscle opposite vertebrae 2, 3, 4, and 5 anterior to the pelvis appear to divide the muscle into five semidistinct parts. The fibers pass posterolaterally to their insertion. (fig. 3).

Origin.—Tendinous by an aponeurosis from the dorsolateral edge of the neural crests of vertebrae 2 to 6 anterior to the synsacrum, deep to the origin of M. rhomboideus superficialis. The origin does not extend as far anteriorly as that of M. rhomboideus superficialis.

Insertion.—Entirely fleshy on the medial surface of the scapula. Posteriorly the dorsal three-fourths of this surface is involved, but in its anterior half the insertion is limited to the dorsomedial edge above the insertions of the slips of M. serratus profundus.

Innervation.—By a twig from the spinal nerve trunk which emerges anterior and lateral to the anterior end of M. serratus profundus; it enters the deep side of the anterior edge. This is the same trunk that serves M. rhomboideus superficialis.

Action.—Pulls the scapula forward and upward toward the midline. Both M. rhomboideus profundus and M. rhomboideus superficialis aid in raising the shoulder. This is important in raising the entire wing while the longitudinal axis of the wing remains horizontal. In soaring and gliding the wing may be raised at its base; this lowers the position of the center of gravity relative to the supporting plane and provides for greater stability.

Comparison.—No significant differences were found among the New World vultures. In *Cathartes* M. serratus profundus inserts partly on the deep surface of M. rhomboideus profundus near the insertion on the scapula.

In *Gymnogyps* and *Coragyps* the muscle is relatively largest (table 18).

M. CORACOBRACHIALIS ANTERIOR

Description.—This triangular muscle lies between the coracoid and the proximopalmar surface of the humerus. It is covered dorsally by the tensor muscles, M. deltoideus minor and the anterior tendon of insertion of M. supracoracoideus (fig. 3).

Origin.—By short fascia from the outer face of the head of the coracoid near the coracohumeral surface and fleshily from the deep side of the long head of M. biceps (fig. 3).

Insertion.—Fleshy on the palmar surface of the humerus proximal to the insertion of M. pectoralis superficialis (fig. 10).

Innervation.—From an anteriorly directed twig of the branch of N. brachialis longus inferior that serves M. biceps.

Action.—Pulls humerus anteriorly and depresses it slightly. The main action probably is at the moment the downstroke begins, when the wing is brought forward, but it also aids in bringing the wing forward to move the center of gravity posteriorly, relative to the wings. It may aid in depressing the anterior edge of the wing.

Comparison.— In *Gymnogyps* and *Vultur* the insertion is somewhat farther distal.

The muscle is almost twice as large relatively in *Gymnogyps* and *Vultur* as in *Cathartes*, *Sarcoramphus* and *Coragyps*. The greater size and more distal insertion in the condors is significant as an adaptation for better soaring.

M. DELTOIDEUS MINOR

Description.—This is a bandlike muscle parallel and anterior to M. deltoideus major. As it crosses the scapuloclavicular articulation and the head of the humerus it covers the insertion of M. supracoracoideus. The direction of its fibers parallels the proximal half of the deltoid crest, and it covers anconally the insertion of M. subcoracoideus.

Origin.—Fleshy from the dorsal part of the head of the scapula posterior to the furcular facet and from the distal outer face of the clavicle dorsal to the coracoid; the main origin is from the scapula (fig. 9).

Insertion.—Fleshy on a wide area on the anteroanconal two-fifths of the deltoid crest proximal to the insertion of M. deltoideus major (fig. 10).

Innervation.—The same branch of N. brachialis longus superior that serves M. deltoideus major and M. tensor patagii brevis sends a twig to the middle of the deep side of the belly.

Action.—Elevates humerus, pulls it anteriorly and raises the anterior edge of the wing. This muscle probably comes into play on the recovery stroke of the wing, at which time the above movements occur simultaneously.

Comparison.—In *Cathartes* the insertion is more proximal.

In *Gymnogyps* the muscle is in two rather distinct parts; the deeper part arises from the scapula; and the superficial layer, arising from the furculum, is situated somewhat farther anterior. The insertion covers the anterior third of the proximal third of the deltoid crest. Opposite the head of the humerus a strong tendon passes posteriorly to insert on the anconal surface of the humerus opposite the middle of M. proscapulohumeralis brevis.

In *Vultur* and *Gymnogyps* the origin and insertion are similar.

The chief origin is from the clavicle in *Sarcoramphus*.

The muscle is best developed in *Gymnogyps;* in *Vultur* it is only one-half as large and is still smaller in *Cathartes*, *Sarcoramphus* and *Coragyps*. The more proximal insertion in *Cathartes*, as compared to the black vulture, reduces the muscle's effectiveness still more. Consequently, the New World vultures listed in order for decreasing effectiveness of M. deltoideus minor for raising the humerus are: *Gymnogyps*, *Vultur*, *Coragyps*, *Sarcoramphus* and *Cathartes*.

M. PROSCAPULOHUMERALIS AND M. SUBSCAPULARIS

Description.—The separate entities of these two muscles are not distinguishable in the vultures. The triangular belly extending from the lateral, ventral and medial surfaces of the scapula to the capital groove of the humerus is made up of three semi-distinct, pennate fasciculi. The belly is covered posteriorly by M. dorsalis scapulae and is covered slightly on its anterior edge by M. proscapulohumeralis brevis. On its proximal lateral edge the posterior fasciculus (probably M. proscapulohumeralis in part) is divided into a deep and a superficial layer by the tendon of insertion of M. serratus anterior.

Origin.—Fleshy from the lateroventral surface of the anterior half of the scapular blade and from the entire width of the medial surface of the anterior third, extending forward to the furcular facet (fig. 9).

Insertion.—Mixed fleshy and tendinous on the entire length of the capital groove of the humerus and on the anterior face of the internal tuberosity, anterior and anconal to the insertion of M. subcoracoideus (fig. 10).

Innervation.—From N. brachialis longus superior. The twigs come off the branch serving the M. dorsalis scapulae.

Action.—Pulls the humerus posteriorly and raises the posterior edge of the wing slightly.

Comparison.—In *Cathartes* the origin on the external face of the scapula extends to the dorsal edge, perhaps as compensation for the shorter scapula. The insertion is limited to the anterior half of the capital groove and does not extend distally on to the internal tuberosity.

In *Gymnogyps* the origin extends ventrally on to the distal half of the inner posterior edge of the coracoid proximal to the scapular articulation. This ventral extension probably represents the origin of the much reduced M. subcoracoideus which is fused to the M. subscapularis.

The muscle in *Vultur* is similar to that in *Gymnogyps*.

The insertion in *Sarcoramphus* is similar to that in *Coragyps*, but it is entirely tendinous.

It is impossible to compare the development of the muscles because M. subcoracoideus in part opposes the action of M. proscapulohumeralis and M. subscapularis; all three are inseparable in *Gymnogyps* and *Vultur*.

The combined Mm. proscapulohumeralis and subscapularis are somewhat larger in *Coragyps* than in *Cathartes*.

M. DORSALIS SCAPULAE

Description.—See figure 3.

Fig. 3. *Coragyps atratus*. Anconal view of the right shoulder and wing, showing a second layer of muscles, ×2/5.

Origin.—Fleshy from the outer face of the posterior three-fourths of the scapula. It covers the entire face posterior and dorsal to the origin of M. proscapulohumeralis (figs. 3 and 9).

Insertion.—By short tendon on the anconal surface of the humerus at the proximal end of the bicipital crest (fig. 10).

Innervation.—A proximal branch of N. brachialis longus superior emerges past the posterior edge of M. proscapulohumeralis and enters the deep side of the distal half of the belly.

Action.—The main function is raising the posterior edge of the wing to decrease the angle of incidence of the wing. Simultaneously it elevates the humerus.

Comparison.— In the other genera the insertion is on the middle of the length of the bicipital crest, and the anterior edge is separated from M. proscapulohumeralis by the additional tendon of origin of the scapular head of M. triceps. In *Vultur* the tendon of insertion is bifurcated.

The muscle is relatively largest in *Sarcoramphus* and *Coragyps*. In *Cathartes* it is smaller; it is somewhat larger in *Gymnogyps* than in *Vultur* (table 18). The point of insertion is of little significance as regards relative ability to tilt the wing, but it is important in raising the wing since a more distal insertion provides a longer power arm. When wing length is considered, it is evident that the muscle in *Coragyps* which possesses the shortest wing is the most efficient for speed. In *Cathartes* and *Sarcoramphus* the muscle is better adapted than in *Gymnogyps;* it is least effective in *Vultur* because of its small size and because the wing is longest in this genus.

M. SERRATUS POSTERIOR

Description.—This complex of fasciculi consists of two layers, the deeper of which probably corresponds to the M. thoracoscapularis of Shufeldt (1890:99). The superficial layer is made up of three fasciculi which are separated only at their dorsal ends. The deep layer is a single broad sheet. The scapular ends of the two dorsal fasciculi and the deep layer are beneath M. dorsalis scapulae. The entire mass is ventral to the scapula, and the fibers pass slightly anteriorly toward their insertion on the scapula (fig. 4).

Origin.—The origin of the three superficial fasciculi is mixed fleshy and tendinous from the fourth true rib. The deep layer arises tendinously from true ribs 2, 3 and 4 below the uncinate processes.

Insertion.—The two dorsal fasciculi of the superficial layer and the entire deep layer attach fleshily to the distal third of the ventral edge of the scapular blade (fig. 9). The ventral superficial slip passes lateral and posterior to the insertion of the dermal component of M. latissimus dorsi and inserts on the skin beneath the posterior end of the humeral feather tract.

Innervation.—Two branches of the roots of N. brachialis longus superior fuse to form a trunk which passes deep to Mm. proscapulohumeralis and dorsalis scapulae over the lateral surfaces of the ribs to enter the deep surface of the deep layer. Some twigs perforate this layer and serve the superficial layer.

Action.—The parts attaching to the scapula tend to pull it ventrally and somewhat posteriorly in opposition to Mm. serratus profundus, rhomboideus profundus and rhomboideus superficialis, but probably a more important function is in inspiration. The ribs are pulled forward and outward to increase the volume of the chest cavity. The dermal component flattens the feathers of the humeral tract; this is important in streamlining the dorsal surface of the wing. Since these feathers are relatively long in the vultures, they form an important part of the supporting surface of the wing. This muscle cooperating with the dermal component of M. latissimus dorsi holds the feathers down against the upward pressure of air beneath the wing and holds them medially to prevent the loss of air next to the body.

Comparison.—The muscle is similar in *Coragyps* and *Cathartes*. In *Gymnogyps* the superficial layer arises from the third and fourth true ribs and is entirely a dermal component; there is no attachment to the scapula. The two dorsal slips attach to the caudal

edge of the posterior part of M. latissimus dorsi, and the ventral part attaches as in *Coragyps*. The deep layer is similar to that in *Coragyps*.

In *Vultur* and *Gymnogyps* the muscle is almost the same, but in the Andean condor the deep layer inserts tendinously on the distal half of the scapular blade. The only fleshy insertion of the deep layer is small and limited to the distal tip of the scapula.

In *Sarcoramphus* only the proximal, dorsal superficial fasciculus of the superficial layer is inserted on the scapula. The other two parts insert on the skin overlying this area, in common with the dermal component of M. latissimus dorsi.

The muscle is relatively largest in *Gymnogyps* and *Sarcoramphus* due in large part to the increased size of the dermal components. It is smallest in *Coragyps* and perhaps insignificantly larger in *Cathartes* and *Vultur*.

M. STERNOCORACOIDEUS

Because of the curved articulation of the coracoid on the sternum, which largely eliminates lateral movements of the coracoid, M. sternocoracoideus, whose sole action is to pull the coracoid laterally and to hold it in the articular groove of the sternum, is vestigial in the New World Vultures. It is an extremely thin sheet extending from the first and second true ribs to the dorsolateral corner of the coracoid (fig. 6). There is no attachment to the sternum. No differences in development were noted among the genera of the Cathartidae.

M. SUBCORACOIDEUS

Description.—Extending from the inner surface of the coracoid to the humerus is the short but strong M. subcoracoideus (fig. 4). Its distal end is ventral to the distal end of M. proscapulohumeralis, and the proximal end is anterior and ventral to the bulk of M. proscapulohumeralis.

Origin.—Fleshy from the anterointernal surface of the coracoid, extending as a wide line from the sternocoracoidal impression to the base of the procoracoid (fig. 4).

Insertion.—Mixed fleshy and tendinous on the proximal surface of the internal tuberosity posterior and palmar to the insertion of M. proscapulohumeralis (fig. 10).

Innervation.—From the most proximal branch of N. brachialis longus superior. The twig enters the middle of the deep side, and another twig serves M. subscapularis.

Action.—Flexes the humerus posteriorly and depresses the posterior edge of the wing. It is more effective in the latter action.

Comparison.—In *Cathartes* and *Sarcoramphus* the insertion is somewhat farther distal. In *Gymnogyps* and *Vultur* the muscle is much reduced and is inseparable from the fused M. proscapulohumeralis and M. subscapularis. The origin extends proximally only 1.5 cm. from the procoracoid.

The muscle is twice as large in *Cathartes* as in *Coragyps* and *Sarcoramphus*, thus indicating that the development may be correlated with the ability to increase the angle of incidence of the wing. However, the absence of the ventral part of the muscle in *Gymnogyps* and *Vultur* greatly reduces the force effective in depressing the posterior edge of the wing. Also, the fusion with the Mm. proscapulohumeralis and subscapularis makes it more difficult for M. subcoracoideus to affect the angle of incidence. I am unable to explain why the two large condors which are superior soarers have a reduced and ill-adapted muscle which is of importance in the delicate tilting of the wing.

M. PROSCAPULOHUMERALIS BREVIS

Description.—This small, short muscle extending from the scapula to the anconal surface of the humerus is covered anconally by M. deltoideus major and the scapular head of M. triceps. It is fleshy throughout (fig. 3).

Origin.—Fleshy from a small area on the ventrolateral edge of the scapula immediately posterior to the glenoid facet (fig. 9).

Insertion.—Fleshy on the distal end of the medial crest on the anconal side of the humeral head anterior to the origin of external head of M. triceps (fig. 10).

Innervation.—The same branch of N. brachialis longus that serves M. proscapulo-

humeralis sends a branch across the lateral face of M. proscapulohumeralis to the proximal fourth of the M. proscapulohumeralis brevis.

Action.—Pulls the humerus posteriorly. Any action is weak.

Comparison.—M. proscapulohumeralis brevis is similar in the vultures, but in *Sarcoramphus* it is much more tendinous than in the other cathartids. It is best developed in *Cathartes* and *Coragyps* and is relatively smallest in *Sarcoramphus* and *Vultur*.

M. SERRATUS PROFUNDUS

Description.—M. serratus profundus is a strong slender muscle composed of three or four semidistinct fasciculi situated between the scapula and the vertebral column deep to the Mm. rhomboideus. The fibers pass posterolaterally to their insertion. (fig. 4).

Origin.—Mixed fleshy and tendinous from the distal tip of the transverse processes of the two posterior vertebrae bearing free ribs and fleshy from the caudal edge of the proximal half of the first true rib.

Insertion.—Fleshy on the middle half of the width of the scapula in the middle third of the length of the scapular blade (fig. 4).

Innervation.—From the most proximal twig of the nerve trunk serving Mm. serrati.

Action.—Pulls the scapula forward and adducts it at the same time. It is thus of importance in moving the shoulder anteriorly, in depressing the anterior edge of the wing and in moving the wing anteriorly as a unit.

Comparison.—In *Cathartes*, *Sarcoramphus*, *Vultur* and *Gymnogyps* the most ventral fasciculus is ventral to the scapula and deep to M. serratus anterior. Consequently, if all the muscle contracts at the same time the main vector of force acts to move the shoulder anteriorly.

M. serratus profundus is relatively largest in *Gymnogyps* and smallest in *Cathartes*, *Sarcoramphus* and *Vultur*.

M. SERRATUS ANTERIOR

Description.—In the cathartids only a single slip is present; Shufeldt (1890:104) found three slips in the raven. The thin flat slip (fig. 4) from the first true rib courses dorsally and anteriorly to divide the M. proscapulohumeralis into a deep and a superficial layer. As it enters M. proscapulohumeralis it becomes tendinous and continues thus to its insertion.

Origin.—Tendinous from the first true rib in the region dorsal to the uncinate process and from the dorsal half of the process itself.

Insertion.—The tendinous insertion is on a longitudinal line on the medioventral corner of the middle of the scapular blade and is surrounded by the origin of M. proscapulohumeralis (fig. 4).

Innervation.—From the same branch of N. brachialis superior that serves M. serratus anterior.

Action.—Any action by this muscle is weak. It may pull the first rib anteriorly and laterally or it may pull the scapula ventrally.

Comparison.—Similar in the genera examined. The muscle is largest in *Coragyps* and smallest in *Sarcoramphus* and *Vultur* (table 18).

M. BICEPS

Description.—This strong fusiform muscle lies obliquely across the palmar surface of the humerus. Anconally it is in part covered by the tendon of M. tensor patagii brevis; proximally on the palmar side it is deep to the tendon of insertion of M. pectoralis superficialis (fig. 2).

Origin.—The wide tendon of the long head originates from the lateral surface of the head of the coracoid deep to the origin of M. coracobrachialis anterior. The short head takes origin tendinously from the entire length of the bicipital crest distal to the ligamental furrow, as Shufeldt (1890:117) described for the raven (fig. 10).

Insertion.—At the level of the brachial impression of the humerus and opposite the

palmar surface of the radius the tendon of insertion divides. The larger, anconal tendon attaches to the posteropalmar corner of the radius 13.5 mm. from the proximal end of the radius. The other branch inserts on the anteropalmar corner of the ulna 19.0 mm. from the tip of the olecranon (fig. 5).

Innervation.—A branch of N. brachialis longus inferior enters the middle of the deep surface.

Action.—The main function is flexion of the forearm, but the humerus is also moved forward. The attachment between the tendinous long head of M. biceps and the tendon of the deep layer of M. pectoralis superficialis is important since it provides a strong tendinous band from the head of the coracoid to the middle of the length of the humerus. This band limits the extent to which the wing may be raised and consequently may aid in holding the wing down in a horizontal position against the pressure of air beneath the wing.

Comparison.—In *Cathartes* the origin of the short head is limited to the distal two-thirds of the bicipital crest; in *Gymnogyps* and *Vultur* the origin is from the proximal end only. The insertion on the radius is the following distance in millimeters from the proximal end of the radius: *Cathartes*, 14; *Sarcoramphus*, 8; *Gymnogyps*, 16; *Vultur*, 13. On the ulna the insertion is 19.3 mm. from the tip of the olecranon in *Cathartes*, 22.0 in *Sarcoramphus*, 30.0 in *Gymnogyps*, and 32.0 in *Vultur*. The ratio of power arm to weight arm is important. The distance the insertion is from the proximal end of the radius and of the ulna is the power arm. The weight arms are the length of the wing distal to the insertion, the length of the radius distal to the insertion and the length of the ulna distal to the insertion.

TABLE 17.—Ratios of Length of Power Arm of M. biceps.

	Per cent of radial length	Per cent of ulnar length	Per cent of wing distal to insertion	
			radius	ulna
Cathartes	9.03	12.19	4.72	6.28
Coragyps	10.11	13.87	4.96	7.12
Gymnogyps	5.78	10.79	3.07	5.91
Vultur	4.10	10.35	2.27	5.77
Sarcoramphus	4.14	11.70	2.25	6.45

All the ratios in table 17 indicate a more distal insertion in *Coragyps* than in *Cathartes*. The insertion in *Vultur* is more proximal than in *Gymnogyps*. A much longer power arm is present in the small vultures than in the large condors.

Relative volumes of M. biceps indicate that it is largest in *Cathartes* and *Sarcoramphus* and smallest in *Coragyps and Gymnogyps*. The differences are small however. Therefore, considering both the size and the power arm the muscle is most effective, as regards power, in *Coragyps* and is slightly less effective in *Cathartes*. The more proximal insertions in *Gymnogyps* and *Vultur* provide for greater speed but less power. Since the muscles are not significantly larger than in the small vultures the power of flexion is considerably less in the condors.

M. DELTOIDEUS MAJOR

Description.—Its posterior edge is superficial to the anterior edge of the scapular head of M. triceps (fig. 1), but it is not attached to M. triceps in the vultures; Shufeldt (1890: 119) described a connection between the two muscles in the raven.

Origin.—Mixed tendinous and fleshy from a wide area on the external face of the scapula between the glenoid and furcular facets and deep to the origin of M. deltoideus minor (fig. 9).

Insertion.—The more proximal insertion is fleshy on the deltoid crest posterior and distal to the insertion of M. deltoideus minor; posteriorly it extends to the insertion of M. latissimus dorsi. Distally it continues 1.5 cm. past the distal end of the deltoid crest (fig. 10). The posterior part of the muscle inserts tendinously on the longitudinal line on the anteroanconal corner of the shaft of the humerus some 1.5 to 2.0 cm. farther distal. This split insertion is the only indication of the double condition described by Shufeldt (1890:117-118).

Innervation.—A twig from the branch of N. brachialis longus superior that serves M. tensor patagii brevis goes to the anterior part of M. deltoideus major. A more distal twig serves the posterior part. The main trunk nerve emerges deep to the scapular head of M. triceps.

Action.—The entire muscle serves to pull the humerus posteriorly and dorsally and to raise the anterior edge of the wing. Because of separate innervation, the parts may contract independently to a certain degree. The anterior part is more important in elevating the leading edge of the wing since the anterior extension of the deltoid crest provides a longer lever arm. The more distal insertion and more caudal origin of the posterior part makes it more effective in pulling the humerus posteriorly.

Comparison.—In *Cathartes* and *Sarcoramphus* the distal insertion is smaller and is 65 mm. from the distal end of the humerus.

In *Vultur*, *Sarcoramphus* and *Gymnogyps* there is an additional tendon of origin from the dorsolateral edge of the middle of the scapula. The tendon is deep to M. latissimus dorsi and superficial to M. proscapulohumeralis. The posterior head is noteworthy since it changes the direction of the muscle, especially the posterior part, and puts it more nearly in the line of force effective in drawing the humerus posteriorly. In the California condor the distal insertion is 105 mm. from the distal end of the humerus; it is 110 mm. in *Vultur*.

The power arm of the distal insertion is 17.8 per cent of the total wing length in *Cathartes*, 19.8 per cent in *Coragyps*, 19.9 per cent in *Gymnogyps* and 19.5 per cent in *Vultur* and *Sarcoramphus*.

Ratios in table 18 show M. deltoideus major best developed in *Sarcoramphus* and *Coragyps;* it is smallest in *Gymnogyps*. Larger size and more distal insertion in *Coragyps*, as compared to *Cathartes*, make the muscle more powerful in pulling the humerus posteriorly. It is impossible to judge the exact effect of the more posterior origin in *Sarcoramphus*, *Gymnogyps* and *Vultur*, but it is unlikely that it compensates completely for the smaller muscles in the condors, as compared to the smaller vultures. Development of M. deltoideus major is apparently correlated with the ability to flap the wings.

M. TRICEPS

Description.—M. triceps consists of three more or less distinct parts which are situated on the posterior surface of the humerus and extend distally across the posterior side of the elbow. The scapular head is a large bandlike muscle anconal to the insertion of M. latissimus dorsi and extending distally parallel to the humerus. In the fourth fifth of the humerus it forms a strong wide tendon; at this point it is joined by the tendon of the small internal head (figs. 1 and 2).

The external head is a heavy pennate muscle lying on the posteroanconal surface of the length of the humerus between the scapular head and M. biceps. In the distal third of the humerus its anterior edge is in contact with the internal head. The internal head is confined to the fourth fifth of the anconal surface of the humerus.

Origin.—The scapular head takes origin tendinously from a narrow longitudinal line on the scapula immediately posterior to the glenoid facet; a strong round tendon forms another origin from the scapula in front of M. latissimus dorsi. The external head originates fleshily from a wide area on the posteroanconal surface of the humerus extending from the bicipital crest to the condyles. In the fourth fifth of the anconal surface the internal head takes fleshy origin from the humerus (fig. 10).

Insertion.—The common tendon of the scapular and internal heads passes through the internal tricipital groove and inserts on the proximal anconal surface of the ulna; it is anconal and anterior to the insertion of the external head which inserts tendinously on the most proximal part of the ulna (fig. 12).

Innervation.—The scapular head is innervated by several twigs of N. brachialis longus superior which enter the middle of the deep side of the belly. The external and internal heads are served by more distal twigs of the same branch, but the external head also receives a series of twigs on its posterior surface from a branch proximal to the branch of the scapular head.

Action.—M. triceps is the powerful extensor of the forearm. The scapular head also moves the wing posteriorly when the forearm is fully extended or when its flexor antagonists at the elbow prevent extension. The scapular head plays a significant role in holding the wing in the semiflexed position used in flex-gliding.

Comparison.—In *Cathartes* the belly of the scapular muscle is three-fourths as long as the humerus, and there is no connection to the internal head. The internal and external heads are inseparably fused and form a bandlike muscle which is much thicker proximally and possesses a wide strong tendon along its posterior border. The internal head evidently has increased in size and extended proximally along the anterior edge of the external head.

In *Gymnogyps* the scapular head has two additional tendons of origin. A weak flat tendon from the humerus 10 mm. proximal to the insertion of M. latissimus dorsi attaches to the anterior edge of M. triceps superficial to M. latissimus dorsi. Another tendon, 1.5 cm. wide extends from the distal edge of M. latissimus dorsi to the deep surface of the scapular head distal to M. latissimus dorsi. The insertion is farther distal than in *Coragyps*. The internal head extends proximally into the middle third of the humeral length.

In *Vultur* the scapular head is the same as in *Gymnogyps*, and the other heads are similar to those in *Cathartes*.

In *Sarcoramphus* the belly of the scapular head is almost as long as the humerus. The internal head is very small and is almost entirely fused to the external head which has a major origin from the middle of the bicipital crest by means of a thin, flat tendon.

M. triceps is relatively largest in *Gymnogyps*. It is weakest in *Cathartes*. In *Vultur*, *Sarcoramphus* and *Coragyps* the development is intermediate between the development in the turkey vulture and in the California condor. The more distal insertion of the scapular head in the condors and the larger size of the entire muscle increases the power of extension; the wing may be maintained in the extended position for long periods as in soaring with less effort on the part of the muscle.

The proximal insertion in *Coragyps*, *Sarcoramphus* and *Cathartes* provides greater speed of extension which is necessary in flapping flight, but the smaller muscle in *Cathartes*, as compared to *Coragyps*, reduces the power available for extension.

M. BRACHIALIS

Description.—Across the palmar side of the elbow is this short wide band of muscle; it lies superficial on the forearm to the insertion of M. biceps but deep to the tendons of origin of Mm. pronator longus and pronator brevis (figs. 2 and 5).

Origin.—Fleshy from the brachial impression on the palmar side of the distal end of the humerus (fig. 10).

Insertion.—Fleshy on the brachial impression on the palmar surface of the ulna 16.0 mm. from the olecranon process (fig. 12).

Innervation.—Twig from N. brachialis longus inferior enters the middle of the palmar surface.

Action.—Flexes forearm on the humerus and depresses the posterior edge of the wing. When flexion of the forearm is prevented by contraction of M. triceps, the M. brachialis is primarily devoted to active depression of the posterior edge of the wing or to holding the forearm horizontal against the great force and leverage of the air on the inferior surfaces of the secondaries.

Comparison.—The muscle is similarly constructed in the New World vultures. In *Gymnogyps* the muscle is three times as large relatively as it is in *Cathartes* and *Sarcoramphus* and two times the size of the muscles in *Coragyps* and *Vultur*. Consequently, it is impossible to correlate the development of M. brachialis with either soaring or flapping flight.

M. EXTENSOR METACARPI RADIALIS

Description.—Two distinct fusiform muscles are situated on the anterior surface of the proximal part of the forearm (fig. 1). These constitute the M. extensor metacarpi radialis. Shufeldt (1890:124-125) stated that the muscle arises by two heads, but that

these unite to form a single large fusiform muscle inserting by a common tendon. In the cathartids the tendons of the two parts do not fuse until they are anterior to the scapholunar. The wide tendon of M. tensor patagii brevis attaches to the tendon of origin of the anconal part; there is little connection to the palmar muscle.

Origin.—The anconal part originates tendinously from the humerus just proximal to the ectepicondylar prominence; the tendon is a fifth of the length of the radius. The palmar part arises fleshily from the same region but proximal to the anconal origin (fig. 1).

Insertion.—After passing through the tendinal groove on the distal anconal surface of the radius the two tendons, now fused, go to their insertion on the anteroproximal part of the extensor process of metacarpal I (fig. 1).

Innervation.—Twigs from N. brachialis longus superior enter the anterior edge of each part.

Action.—Because it is chiefly tendinous the anconal muscle may act as an automatic extensor of the hand when the forearm is extended. The fleshy palmar muscle may also act as a tendon, but it is useful in active extension of the hand and in flexion of the forearm.

Comparison.—In *Cathartes* and *Sarcoramphus* the anconal part is limited to the second quarter of the radial length. In *Vultur* and *Gymnogyps* the parts are more nearly equal in size than in *Coragyps*, but the palmar muscle is still larger.

Ratios of relative volumes (table 18) indicate that the muscle is best developed in *Coragyps* and *Gymnogyps;* it is significantly smaller in *Cathartes, Vultur* and *Sarcoramphus.*

M. EXTENSOR DIGITORUM COMMUNIS

Description.—The belly is situated on the posteroanconal surface of the proximal half of the radius. At the external condyle of the ulna the tendon turns posteriorly to the metacarpus. Opposite the base of phalanx 1, digit I the tendon branches superficial to the small belly of M. flexor metacarpi brevis (fig. 1).

Origin.—By long tendon from the ectepicondylar prominence of the humerus in common with but superficial to the origins of Mm. supinator brevis, anconeus, extensor metacarpi radialis and flexor metacarpi radialis (fig. 10).

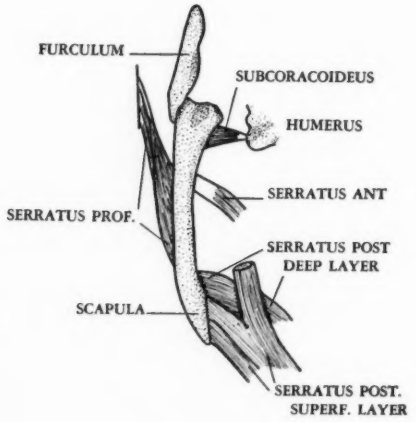


Fig. 4. *Coragyps atratus.* Dorsal view of the deep muscles of the right shoulder, ×1/2.

Insertion.—The small anterior branch passes anteriorly to insert on the posteroanconal corner of digit I, 5.0 mm. from the proximal end. The main branch continues out the anteroanconal surface of metacarpal II in the tendinal groove and attaches to the anteroanconal part of the base of phalanx 1, digit II (fig. 13).

Innervation.—The postradial branch of N. brachialis longus superior sends a twig to the middle of the deep side of the muscle.

Action.—Weak flexion of the forearm and extension of the hand. Digit I is flexed posteriorly, and digit II is extended; both are moved anconally. The approximation of these digits is important since it flattens the alula against the forepart of the wing and thereby increases the speed of soaring or gliding flight and decreases the lifting power (p. 551). Acting as a tendon the muscle functions as an automatic extensor of the manus when the forearm is extended.

Comparison.—The muscle is similar in the various vultures. It is somewhat better developed in *Cathartes* and *Coragyps* than in the condors and the royal vulture.

M. SUPINATOR BREVIS

Description.— See figure 1.

Origin.—Tendinous from a small area on the ectepicondylar prominence of the humerus deep to the origin of M. extensor digitorum communis (fig. 10).

Insertion.—Mixed fleshy and fascial on a large area of the anterior face of the proximal part of the radius (fig. 11).

Innervation.—A twig from the anterior branch of N. brachialis longus superior enters the deep anterior edge of the muscle just before the nerve disappears beneath the muscle.

Action.—Flexes the forearm and elevates the anterior edge of the wing.

Comparison.—In *Cathartes*, *Gymnogyps*, *Sarcoramphus* and *Vultur* the muscle is limited to the proximal third of the radius.

The muscle is much the largest in proportion to the total wing musculature in *Gymnogyps*. In *Vultur* it is larger than in *Coragyps* and *Sarcoramphus;* it is smallest in *Cathartes*. In *Coragyps*, as compared to *Cathartes*, the larger size and more distal insertion make possible more powerful flexion of the forearm, as is necessary in flapping flight. In *Gymnogyps* and *Vultur* the large muscle together with the proximal insertion give greater speed, and perhaps as much power as in *Coragyps*. It is probable that in the large condors the muscle functions mainly to raise the anterior edge of the wing, and the increased size of the muscle is an adaptation for this purpose; in this action the point of insertion along the longitudinal axis of the wing is of no importance. It is the anteroposterior location that is significant; no differences were found in this regard.

Therefore, for soaring and gliding flight the muscle is best adapted in *Gymnogyps*. In *Vultur* it is next best developed. In *Cathartes* it is most poorly developed for any type of flight.

M. FLEXOR METACARPI RADIALIS

Description.—The fusiform belly is situated in the second and third quarters of the ulnar length (fig. 1).

Origin.—Tendinous from the ectepicondylar prominence of the humerus distal to the origin of M. extensor digitorum communis and in common with the origin of M. anconeus (fig. 10). There is strong fascial attachment to the proximal anterior part of the ulna but no definite tendon as Shufeldt (1890:128) found in the raven. However there are three tendinous slips which pass posteriorly from the tendon of origin to cross the ulna and attach to the aponeurosis surrounding the bases of the medial secondaries (fig. 1); these may perhaps be considered a part of the insertion.

Insertion.—Tendinous on the flexor prominence on the posterior anconal corner of metacarpal II slightly more than a third of the way out this bone (fig. 13).

Innervation.—Three twigs from the anterior branch of N. brachialis longus superior enter the deep surface of the muscle. These twigs come off distal to the twig to M. extensor digitorum communis.

Action.—Flexes the forearm and manus.

Comparison.—Opposite the proximal end of metacarpal II the tendon of insertion in *Cathartes* bifurcates. The small additional posterior tendon goes to the fascia overlying the proximal third of the anconal side of M. flexor metacarpi posterior. This weak tendon aids in pulling the distal ends of the medial primaries toward the secondaries. In *Sarcoramphus* the inserting tendon, besides attaching to metacarpal II, is continuous with the central tendon of M. interosseous dorsalis.

In *Gymnogyps* the belly is in the proximal three-fourths of the radial length; its tendon of origin is shorter. The muscle is largest in *Gymnogyps;* in *Cathartes* it is only a fifth as large relatively; in *Sarcoramphus* it is one-half as large. In *Vultur* and *Coragyps* the muscle is approximately two thirds as large as in *Gymnogyps* (table 18).

M. PRONATOR BREVIS

Description.—The strong fusiform belly of this muscle extends distally two-fifths to one-half of the way out the radius (fig. 2).

Origin.—By wide strong tendon from the internal condyle of the humerus above the entepicondylar prominence and 3.0 mm. proximal to the origin of M. pronator longus (fig. 10).

Insertion.—Tendinous and fleshy on a line 23.0 mm. long on the anteropalmar edge of the radius (fig. 11). The distal end of the insertion is 85.0 mm. from the distal end of the radius.

Innervation.—Twigs from N. brachialis longus inferior enter the deep edge of the muscle on either side of the insertion of M. biceps.

Action.—Although the insertion makes possible the depression of the anterior edge of the wing, in soaring and gliding flight little use need be made of this action. Air pushing upward on the lever arm provided by the long secondaries constantly tends to rotate the anconal surface of the wing anteriorly. M. pronator brevis is of more importance in flexing the forearm.

Comparison.—The distal end of the insertion is the following distances from the distal end of the radius: *Cathartes*, 112.0 mm.; *Sarcoramphus*, 123.0; *Gymnogyps*, 198.0; *Vultur*, 203.0. In *Sarcoramphus*, *Gymnogyps* and *Vultur* the distal part of the insertion is thin and weak, but the muscle is thickened into a cylinder proximally.

The insertion is most distal in *Coragyps* (distal end is 41.2 per cent of the way distally on the radius); in *Cathartes*, 34.5 per cent; in *Gymnogyps*, 32.4 per cent, and in *Vultur* and *Sarcoramphus*, 37.6 per cent. Consequently, for flexion of the forearm *Coragyps* possesses the longest power arm. The weakness of the distal part of the insertion in *Vultur*, *Sarcoramphus* and *Gymnogyps* shortens the effective part of the lever arm.

In *Vultur* the muscle is relatively three-fourths as large as in the other genera. Therefore, considering both the lever arm and the power of the muscle for flexion, *Coragyps* may most easily flex the forearm. *Sarcoramphus* is next most able, and *Vultur* is least able to flex the forearm. Power of this muscle may be correlated with the ability to flap.

M. PRONATOR LONGUS

Description.—See figure 2.

Origin.—By strong round tendon from the entepicondylar prominence of the internal condyle of the humerus distal to the origin of M. pronator brevis but proximal to and partly overlapped by the tendinous origin of M. flexor carpi ulnaris (fig. 10).

Insertion.—The insertion is 3.0 mm. wide and 40.0 mm. long on the anteropalmar part of the radius and the adjoining belly of M. extensor indicis longus, palmar and posterior to the insertion of M. pronator brevis (fig. 11).

Innervation.—Two twigs of the anterior branch of N. brachialis longus inferior go to the muscle distal to the insertion of M. biceps and distal to the twig to M. pronator brevis.

Action.—Because of its more distal origin and more posterior insertion on the radius, M. pronator longus is less effective than M. pronator brevis for flexion and for depression of the anterior edge of the forearm. It functions primarily to flex and depress the forearm.

Comparison.—The muscle is similar throughout the New World vultures. *Coragyps* and *Gymnogyps* possess the best development.

M. EXTENSOR POLLICIS LONGUS

Description.—In contrast to the condition in the raven (Shufeldt, 1890:132-133), this muscle is relatively large and has a strong tendon. The pennate belly which is deep to Mm. anconeus and flexor metacarpi radialis is half as long as the radius. Proximally the belly is pierced by the anterior branch of N. brachialis longus (fig. 3).

Origin.—Fleshy from a line on the ulnar-palmar surface of the proximal half of the radius and from the palmar surface of the ulna; the ulnar origin is much larger and longer (fig. 12).

Insertion.—The tendon passes through the tendinal groove on the distal end of the radius deep to the other extensor tendons and inserts on the extensor process of metacarpal I beneath the tendon of M. extensor metacarpi radialis (fig. 13).

Innervation.—Twigs of the anterior branch of N. brachialis longus superior enter the anterior edge of the proximal quarter of the muscle next to the radius.

Action.—A strong extensor of the hand.

Comparison.—In *Cathartes* the belly is two-thirds of the length of the forearm, and the radial origin is smaller than in *Coragyps*. The insertion is anconal to the insertion of M. extensor metacarpi radialis; thus the hand is elevated as well as extended.

The ulnar and radial origins are of equal length in the California condor, but the rest of the muscle is like that in *Cathartes*.

In *Vultur* the muscle is as in *Coragyps* except that the belly is three-fifths of the radial length.

In contrast to the other cathartids, the radial origin is longer in *Sarcoramphus*, and the belly of the muscle is three-fourths the length of the radius.

Ratios in table 18 indicate that the muscle is relatively largest in *Gymnogyps*, somewhat smaller in *Coragyps*, intermediate in *Cathartes* and *Vultur*, and smallest in *Sarcoramphus*.

M. ANCONEUS

Description.—This powerful, partly pennate muscle passes across the elbow joint and halfway out the ulna. Anconally it is in part covered by M. flexor metacarpi radialis. The deep anterior edge is in contact with M. extensor pollicis longus (fig. 3).

Origin.—By strong tendon from the ectepicondyle of the humerus distal to the origin of Mm. extensor digitorum communis and supinator brevis. The tendon is deep to and intimately connected with the tendinous origin of M. flexor metacarpi radialis (fig. 10).

Insertion.—The area of insertion is 60.0 mm. long and starts 23.0 mm. distal to the proximal tip of the olecranon; proximally it is 6.0 mm. wide. It extends, at the proximal end only, on to the palmar surface of the ulna immediately dorsal to the origin of M. extensor pollicis longus (fig. 12).

Innervation.—Two twigs of N. brachialis longus superior enter the first third of the anterior edge of the muscle.

Action.—The main function is flexion of the forearm, but it also elevates the forearm slightly.

Comparison.—In *Cathartes* the origin is 50.0 mm. long and starts 32.0 mm. from the olecranon; in *Gymnogyps* it is 90.0 mm. long and 42.0 mm. distal; in *Vultur*, 104.0 mm. long and 42.0 mm. distal, in *Sarcoramphus*, 75.0 mm. long and 29.0 mm. distal to olecranon.

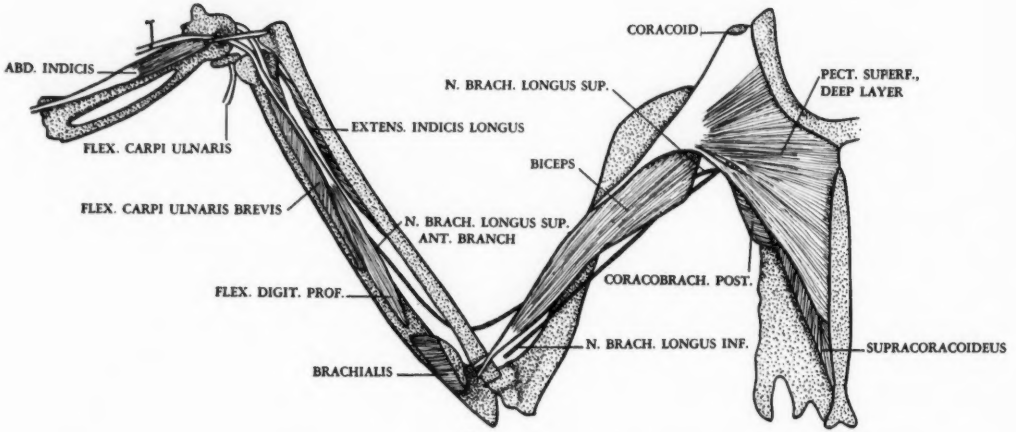


Fig. 5. *Coragyps atratus*. Palmar view of the right wing and breast, showing a second layer of muscles, ×2/5

Consequently, the power arm, in relation to ulnar length, is longest in *Coragyps* (53.2 per cent), next longest in *Sarcoramphus* (49.5) and *Cathartes* (47.4) and shortest in *Gymnogyps* and *Vultur* (42.8). The differences in the length of the power arm between *Coragyps* and *Cathartes* and between *Coragyps* and the condors are even greater when the increased length of the metacarpus and digits in the turkey vulture and the condors is considered.

The muscle is best developed in *Gymnogyps* and is least developed in *Cathartes* and *Sarcoramphus*. In *Coragyps* it is larger than in *Vultur*. When the length of the wing distal to the elbow, the length of the power arm, and the relative development of the muscle are considered it is apparent that in *Coragyps* flexion of the forearm is easiest. *Gymnogyps* possesses greater ability for flexion than do *Sarcoramphus*, *Vultur* and *Cathartes*.

M. EXTENSOR INDICIS LONGUS

Description.—On the metacarpal the tendon is directed obliquely anteriorly so that as it goes to digit II it is on the anterior face of phalanx 1. Opposite the proximal end of the metacarpus it goes through a small tendinous sling attached to the posteroanconal corner of the scapholunar. Between the first and second thirds of metacarpal II the tendon of insertion is joined on its anterior edge by the tendon of M. flexor metacarpi brevis (figs. 1-3).

Origin.—Fleshy from a narrow line on the ulnar-palmar surface of the radius in the third and fourth fifths of this bone (fig. 11).

Insertion.—By wide strong tendon on the anterior surface of the base of phalanx 2 of digit II (fig. 14).

Innervation.—From the anterior branch of N. brachialis longus superior.

Action.—Extension of digit II.

Comparison.—In *Sarcoramphus* the insertion is a third of the way out phalanx 2 which gives greater efficiency in extending the digit. Proximally the muscle is continuous with a part of M. pronator longus. The muscle is largest in *Coragyps* and *Gymnogyps* and smallest in *Vultur* and *Cathartes* (table 18.)

M. FLEXOR DIGITORUM SUBLIMIS

Shufeldt (1890:137) gave a very sketchy description of this muscle and did not illustrate it in his drawings. No muscle in the vultures fills the requirements of Gadow's description of M. flexor digitorum sublimis, and it is likely that in the raven as well as in the New World vultures the muscle is represented in part by the wide tendon of the anterior part of M. flexor carpi ulnaris.

M. FLEXOR DIGITORUM PROFUNDUS

Description.—The small slender belly forms a tendon at the beginning of the distal third of the forearm (fig. 5). On the metacarpus the tendon courses anterior to the pisiform process and beneath the ligament from the anteropalmar tip of the radius to the pisiform process; it then continues on the anteropalmar edge of the metacarpus and digit II to its insertion (fig. 14).

Origin.—Fleshy from the anteropalmar surface of the middle of the ulna (fig. 12).

Insertion.—Tendinous on the palmar side of the base of phalanx 2, digit II. The insertion is approximately a third of the way posterior on this surface (fig. 14).

Innervation.—From the anterior branch of N. brachialis longus inferior on the radial side of the proximal third of the belly.

Action.—Flexes the hand, but the main function probably is to extend and depress digit II as in flex-gliding.

Comparison.—In the other genera, except *Sarcoramphus*, the insertion is on the anteropalmar corner of the base of phalanx 2. This decreases the ability to depress, but increases the ability to extend, the digit.

The muscle is relatively largest in *Gymnogyps* (table 18). It is smallest in *Cathartes* and only slightly larger in *Coragyps* and *Sarcoramphus*. In *Vultur* the size is intermediate between *Gymnogyps and Coragyps*. In the development of this muscle, as in many muscles affecting the distal parts of the wing, one finds a correlation with the type of flight. The master soaring types, the condors, possess larger muscles to provide for better control of the broad tip of the wing.

M. FLEXOR CARPI ULNARIS

Description.—This muscle complex is composed of three distinct parts which are situated on the posteroanconal part of the forearm next to the ulna (figs. 1 and 2). The posterior part has a superficial slip which gives rise to tendon halfway out the forearm and a larger deeper pennate slip extending distally four-fifths the length of the ulna. This latter tendon inserts on the large flat tendon of the superficial slip of the posterior part.

The long, slim belly of the anterior muscle is excavated posteriorly to accommodate the anterior edge of the posterior part. The wide tendon is superficial and continuous from the origin to the insertion on the cuneiform. Beneath it the deeper part is pennate (figs. 1 and 2).

Origin.—The posterior muscle originates by a round tendon 4.0 mm. long from a pit on the entepicondyle. The anterior part arises similarly, proximal to the origin of the posterior part (fig. 10).

Insertion.—A strong wide tendon from the posterior muscle inserts on the distal posterior edge of the cuneiform; there are no branches. The superficial tendon attaches to the proximal anterior edge of the cuneiform; the smaller deeper tendon of the anterior muscle runs across the palmar surface of the cuneiform around its distal edge, and out the anteropalmar surface of metacarpal II to insert on the anterior face of the middle of phalanx 2 of digit II (fig. 13). Halfway out its length and opposite the distal end of metacarpal II the tendon passes beneath the tendon of M. flexor digitorum profundus but does not fuse with it, as it does in the raven (Shufeldt, 1890:142).

Innervation.—Twigs of N. brachialis longus inferior pass deep to the anterior muscle to enter the deep side of the posterior part; there are separate twigs to the two parts of the posterior muscle. The anterior muscle is served in the proximal half of its belly by branches from the posterior trunk of N. brachialis longus inferior.

Action.—The wide superficial tendon extending from the humerus to the cuneiform acts as an automatic device to hold the wing in an extended position once the wing has been moved into this position by action of other muscles. The small tendon of the anterior muscle extends the hand and flexes the forearm, and the posterior muscle parts are powerful flexors of the forearm and hand.

Comparison.—The muscle is similar throughout the cathartids, but in *Cathartes*, *Gymnogyps*, *Sarcoramphus* and *Vultur* the insertion of the deep part of the anterior muscle is on the distal end of the anterior face of phalanx 2 of digit II. Thus the power arm for extension of the index digit is significantly longer than in *Coragyps*.

The ratios in table 18 demonstrate that the muscle is best developed in *Gymnogyps* and is least developed in *Sarcoramphus* and *Cathartes;* it is slightly larger in *Coragyps* and *Vultur* than in *Cathartes*. However, the tendon for holding the wing extended is relatively larger in *Gymnogyps*, *Cathartes*, *Sarcoramphus* and *Vultur* than in *Coragyps*, as is the deep part of the anterior muscle which extends digit II.

M. FLEXOR CARPI ULNARIS BREVIS

Description.—The tendon which is formed near the distal end of the ulna passes across the anteropalmar corner of the ulna and the distal palmar and anterior surfaces of the cuneiform. In the region of the wrist it is held in place by strong fascia and by a

ligament from the distal end of the radius to the pisiform process of the metacarpus (fig. 5).

Origin.—Fleshy from the palmar side of the distal half of the ulna. Distally the origin extends on to the radial surface, and even on to the anconal surface of the ulna (fig. 12).

Insertion.—Tendinous on the middle of the proximal edge of the anconal surface of the metacarpus (fig. 13).

Innervation.—The anterior branch of N. brachialis longus inferior sends a twig to the middle of the anconal edge of the belly.

Action.—When the manus is completely extended, this muscle is capable of flexing it through approximately sixty degrees. At this point flexion ceases and the anterior edge of the hand is depressed in a rotatory movement, as far as is permitted by the articulation of the bones. Thus the muscle is useful in tilting the distal parts of the wing to decrease the angle of incidence and to provide a gentle gliding slope. It may also be employed in banking in which depression of the anterior edge of the manus and its attached primaries causes decreased lifting power which in turn causes the entire wing to drop lower and turn the bird toward that side (p. 551).

It is a noteworthy fact that in broad-winged soaring birds the distal parts of the wing accomplish most of the delicate adjustments necessary to successful flight. This eliminates the necessity of adjusting the entire wing which would require impossible bulk in the musculature. Short, narrow wings usually accompany great speed and agility in flapping flight because they may be rotated, moved vertically and horizontally, and tilted more easily than long, broad wings. Possession of relatively long and wide wings makes flapping flight arduous in the New World vultures.

Comparison.—In *Cathartes*, *Gymnogyps*, *Sarcoramphus* and *Vultur* the muscle is limited to the distal two-fifths of the ulnar length.

M. flexor carpi ulnaris brevis is largest in *Coragyps* and *Cathartes* and is smallest in *Vultur* and *Sarcoramphus* (table 18). Judging from relative size alone, development of the muscle may be correlated with the ability to flap. However, as indicated above, this muscle is important in both flapping and soaring flight because it produces movements vital to both types of flight. Hence no correlation with type of flight is possible.

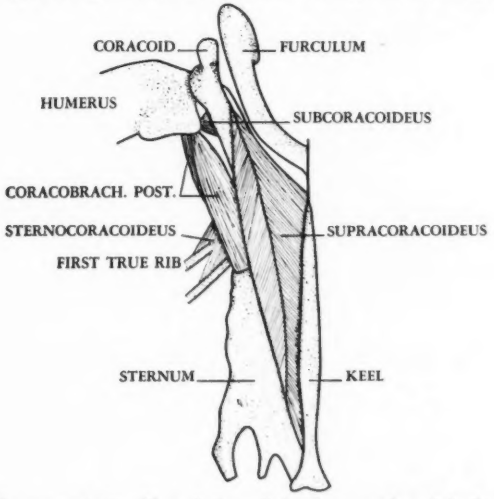


Fig. 6. *Coragyps atratus*. Ventral view of the deep muscles of the breast. ×1/2.

M. ABDUCTOR POLLICIS

Description.—This short muscle is situated on the palmar surface of the proximal end of the metacarpus posterior and proximal to the extensor process (fig. 2).

Origin.—Tendinous from the palmar anterior edge of the inserting tendon of M. extensor metacarpi radialis proximal to the extensor process (fig. 2).

Insertion.—Fleshy on the proximopalmar corner of the pollex and tendinous on the anterior surface of the digit approximately halfway out this bone (fig. 13).

Innervation.—From the anterior branch of N. brachialis longus inferior.

Action.—Extends and depresses digit I. Because of the origin on the tendon of M. extensor metacarpi radialis the muscle may function as a tendon when the long extensor contracts.

Comparison.—The muscle is similar in *Cathartes*. In *Vultur* the tendinous insertion is one-fourth of the way distally on the digit. In *Gymnogyps* the only insertion is at the distal end of the anterior surface of the pollex; in *Sarcoramphus* it is halfway out the pollex.

The muscle is larger in *Cathartes* than in *Gymnogyps*, but the more distal insertion in the latter more than offsets the larger muscle in the turkey vulture. In *Coragyps* the muscle is relatively smallest, but power to extend and depress the digit is about the same in *Vultur* and *Coragyps* because the power arm is much shorter in the Andean condor. Consequently, the muscle is most powerful in *Gymnogyps* and only slightly less effective in *Cathartes* and *Sarcoramphus*. In *Coragyps* and *Vultur* the muscle action is significantly weaker.

M. ADDUCTOR POLLICIS

Description.—M. adductor pollicis is a triangular muscle extending from metacarpal II to the pollex. The fibers converge as they pass anterodistally (fig. 1).

Origin.—The origin is mixed fleshy and tendinous from a line 13.0 mm. long on the anteropalmar edge of metacarpal II immediately distal to the fusion of metacarpals I and II (fig. 14).

Insertion.—Mixed fleshy and tendinous on the distal posterior surface of digit I (fig. 13).

Innervation.—From the anterior branch of N. brachialis longus inferior.

Comparison.—In *Cathartes*, *Sarcoramphus*, *Gymnogyps* and *Vultur* the origin is farther distal by a third of its width. In *Gymnogyps*, *Sarcoramphus* and *Vultur* the main insertion is on the bases of the alular feathers and is thus farther posterior which increases the vector of force effective in pulling the alula toward the palmar surface. In the turkey and royal vultures and in the California and Andean condors the more distal origin, as compared to *Coragyps*, decreases the force wasted in end thrust against metacarpal I.

The larger size of the muscle in *Cathartes*, as compared to the condors and *Sarcoramphus*, makes easier the flexion posteriorly, but the more anterior insertion lessens the power to pull the alula down against the anterior edge of the wing. There are no differences between *Gymnogyps*, *Sarcoramphus* and *Vultur*. In *Coragyps* the short power arm and the small muscle combine to provide this vulture with the least ability to flex the pollex.

Development of M. adductor pollicis is correlated with the ability to soar and glide.

M. FLEXOR DIGITI III AND M. FLEXOR BREVIS DIGITI III

Description.—These two muscles are considered as one in this study because M. flexor brevis digiti III, if it is present, is continuous distally with M. flexor digiti III and is indistinguishable from it (fig. 2). Shufeldt (1890:150) noted the rudimentary ligamental nature of the brevis part in the raven. Evidently the muscle is even less developed in the

New World vultures. The ligament connecting metacarpal III and digit III perhaps represents M. flexor brevis digiti III (fig. 2).

Origin.—Mixed fleshy and tendinous from the posterior proximopalmar edge of metacarpal III, but extending posteriorly to the distal end of the metacarpal on the posterior surface (fig. 13).

Insertion.—Fleshy and tendinous on the posterior extension of the phalanx of digit III (fig. 14).

Innervation.—From the most distal tip of the medial branch of N. brachialis longus inferior.

Action.—Since the single phalanx of digit III is tightly bound by ligaments to phalanx 1 of digit II this muscle flexes digits II and III.

Comparison.—The configuration is similar in the cathartid genera. The muscle is relatively largest in *Gymnogyps* and smallest in *Coragyps and Sarcoramphus*. In *Cathartes* and *Vultur* the development is intermediate between *Coragyps* and *Gymnogyps*.

M. ABDUCTOR DIGITI II

In the new World vultures M. abductor digiti II is represented only by a ligament extending distally from the distal anteropalmar edge of the metacarpus to the posteropalmar edge of phalanx 1, digit II where it is attached between the first and second thirds of the length of the phalanx (fig. 2). Its only action is to hold phalanx 1 in place.

M. FLEXOR METACARPI BREVIS

Description.—M. flexor metacarpi brevis is a small, easily overlooked muscle on the anconal aspect of the wrist and proximal part of metacarpal II. It is deep to the tendons of Mm. flexor carpi ulnaris and extensor digitorum communis (fig. 3).

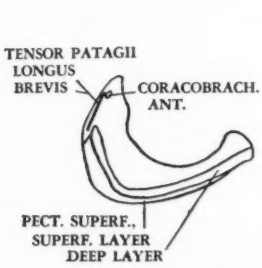


Fig. 7. *Coragyps atratus*. Lateral view of furculum showing attachments of muscles, ×1/2.

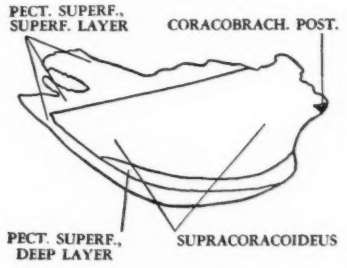


Fig. 8. *Coragyps atratus*. Lateral view of sternum showing attachments of muscles, ×1/2.

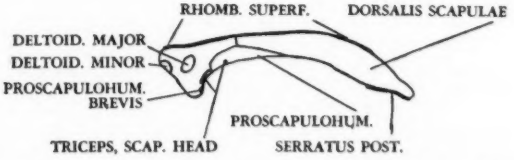


Fig. 9. *Coragyps atratus*. Lateral view of scapula showing attachments of muscles, ×1/2.

Origin.—Tendinous from the distoanconal corner of the scapholunar (fig. 3).

Insertion.—One-third of the way out the anconal side of metacarpal II the small tendon fuses to the anterior edge of the tendon of M. extensor indicis longus (fig. 3).

Innervation.—From a twig of the anterior branch of N. brachialis longus superior.

Action.—Any action is weak, but the muscle tends to flex and elevate digit II and the entire manus.

Comparison.—The muscle is similar throughout the cathartids. It is twice as large in *Cathartes* as in *Coragyps* and *Sarcoramphus* and twice as large in *Gymnogyps* as in *Vultur*. In *Gymnogyps* the muscle is only slightly more than half the size it is in *Cathartes*.

Gadow (1890:27) stated that the muscle often sends tendons to the primaries. One such vestigial tendon was found in *Cathartes*.

M. INTEROSSEUS DORSALIS

Description.—This is the anconal member of a pair of pennate muscles lying in the intermetacarpal space (fig. 1). It is separated from M. interosseus palmaris throughout its length by the anterior branch of N. brachialis longus superior.

Origin.—Fleshy from a line on the posterior surface of metacarpal II and a line on the anterior surface of metacarpal III (fig. 13).

Insertion.—The tendon which is formed at the distal end of the intermetacarpal space passes obliquely outward across the midanconal surface of phalanx 1, digit II to insert on the anteroanconal part of the base of phalanx 2.

Innervation.—A twig from the anterior branch of N. brachialis longus superior enters the middle of the deep side of the muscle.

Action.—Extension and elevation of digit II, especially phalanx 2.

Comparison.—Although the muscle is similarly formed in the different vultures its development shows a graded series from largest in *Cathartes* and *Sarcoramphus*, through *Coragyps* and *Gymnogyps* to smallest in *Vultur*.

M. INTEROSSEUS PALMARIS

Description.—The muscle is immediately palmar to M. interosseus dorsalis, is pennate and is smaller. It forms a tendon in the distal third of the intermetacarpal space (fig. 2).

Origin.—Fleshy on a line on the posteropalmar edge of metacarpal II and the anteropalmar edge of metacarpal III (fig. 14).

Insertion.—The tendon runs between the distal ends of metacarpals II and III and between the proximal ends of digits II and III to cross the palmar surface of phalanx 1 of digit II and follow the posterior edge of phalanx 2 to its insertion approximately halfway out this phalanx (fig. 14).

Innervation.—From the anterior branch of N. brachialis longus superior which separates M. interosseus palmaris and M. interosseus dorsalis.

Action.—Opposes M. interosseus dorsalis by flexing digit II, but aids it in elevating the digit.

Comparison.—In *Cathartes* and *Vultur* the tendon is formed at the distal end of the intermetacarpal space. In *Gymnogyps* the muscle is one and one-half times as large as it is in *Cathartes*, *Sarcoramphus* and *Vultur* and twice as large as in *Coragyps*.

M. EXTENSOR POLLICIS BREVIS

Description.—This small muscle arises fleshily from the proximoposterior anconal surface of metacarpal I and passes obliquely outward to insert tendinously on the anteroanconal side of the base of the pollex (fig. 1).

Innervation.—Small twig of the anterior branch of N. brachialis longus superior.

Action.—Raises and abducts the thumb.

Comparison.—Similar in the vultures. In *Coragyps* and *Cathartes* it is relatively two-thirds as large as in *Gymnogyps;* in *Vultur* it is only a fourth as large as in the California condor, and only a third as large in the royal vulture.

M. ABDUCTOR INDICIS

Description.—On the palmar surface of metacarpal II is this relatively large muscle whose contractile elements are confined to the proximal one-half of the metacarpal. As it passes distally it runs anteriorly to cross the anteropalmar surface of the distal end of metacarpal II in its own pronounced groove (fig. 5).

Origin.—Fleshy from the palmar side of metacarpal II, extending distally from the pisiform process to the middle of the length of the bone. (fig. 14).

Insertion.—Tendinous on the anteropalmar corner of the base of phalanx 1, digit II.

Innervation.—From the anterior branch of N. brachialis longus inferior.

Action.—Depresses and extends the index digit.

Comparison.—In *Cathartes* the belly is almost as long as the metacarpus; in *Vultur* and *Sarcoramphus* it is three-fourths as long. In *Gymnogyps* the insertion is on the anteroanconal corner of the base of phalanx 1 of digit II.

The muscle is largest in *Vultur* and smallest in *Coragyps*. It is larger in *Gymnogyps* than in *Sarcoramphus* and *Cathartes*.

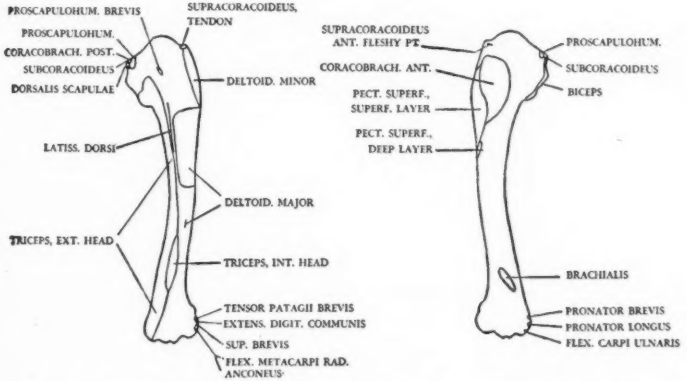


Fig. 10. *Coragyps atratus.* Anconal and palmar views of humerus showing attachments of muscles, ×1/3.

M. ABDUCTOR INDICIS BREVIS

Description.—Present only in *Coragyps.* This very small muscle is situated on the distal half of the palmar surface of metacarpal II and is completely covered by M. abductor indicis (fig. 14). The muscle undoubtedly arose as a deep fasciculus of M. abductor indicis because there is no other possible origin and because the two muscles are served by the same twig of N. brachialis longus inferior.

Origin.—Fleshy from the palmar surface of metacarpal II; it constitutes a distal continuation of the origin of M. abductor indicis.

Insertion.—Tendinous on the anteropalmar corner of the base of phalanx 1, digit II deep to the insertion of M. abductor indicis.

Action.—Depresses and extends the index digit.

M. FLEXOR POLLICIS

Description.—A small muscle situated on the palmar surface of the base of the metacarpus; it lies between the pisiform process and M. abductor pollicis which overlies it in part (fig. 2).

Origin.—Fleshy from the fused area of metacarpals I and II anterior to the pisiform process (fig. 14).

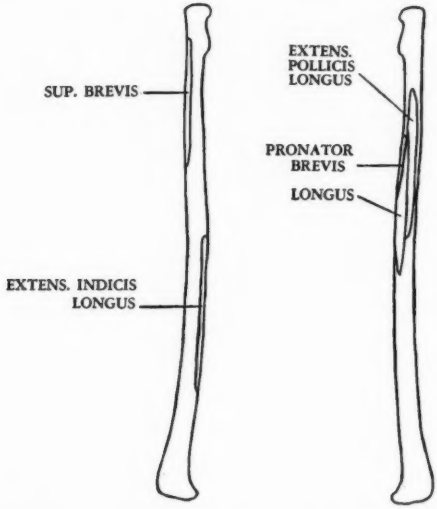


Fig. 11. *Coragyps atratus.* Anterior and posterior views of radius showing attachments of muscles, ×1/2.

Insertion.—Tendinous on the posteropalmar corner of the base of the pollex (fig. 2).

Innervation.—Twig from the anterior branch of N. brachialis longus inferior which passes anterior to the pisiform process.

Action.—Pulls the alula down and flexes it posteriorly. It is important in holding the alula next to the rest of the hand and in depressing it from its raised position which is so frequently observed in soaring.

Comparison.—Similar throughout the New World vultures. The M. flexor pollicis is best developed in *Cathartes* in which it is twice as large relatively as in *Gymnogyps* and *Sarcoramphus.* In *Coragyps* the muscle is slightly larger than in *Vultur;* in both forms the muscle is less than one-third as large as in *Cathartes.*

M. FLEXOR METACARPI POSTERIOR

Description.—It is a tripartite mass situated along the posterior edge of the manus (fig. 1). Distally it is posterior to M. flexor digiti III from which it may have split off. Shufeldt (1890:149) noted that in the raven a few fibers of M. flexor digiti III arose from the ulna. This origin corresponds to the origin of the muscle considered here.

The central, palmar fasciculus is the largest, and the posterior anconal slip is the smallest (fig. 1).

Origin.—By a single wide tendon from the distal anteroanconal surface of the ulna (fig. 12).

Insertion.—The anterior anconal slip inserts fleshily on the posterior surface of metacarpal III immediately proximal to the origin of M. flexor digiti III (fig. 1). The pos-

Innervation.—From the posterior branch of N. brachialis longus superior.
terior anconal fasciculus inserts on the medial surface of the base of the innermost

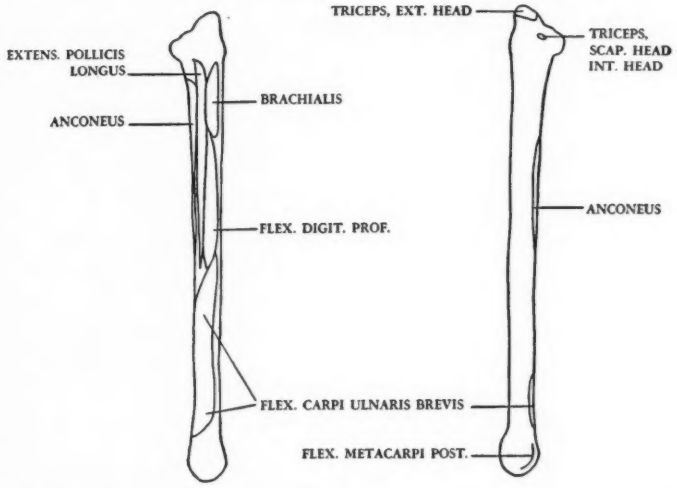


Fig. 12. *Coragyps atratus.* Anterior and posterior views of ulna showing attachments of muscles, ×9/20.

primary. The large palmar fasciculus inserts tendinously on the palmar surfaces of the bases of primaries 2, 3, 4, 5 and 6.

Action.—The posterior anconal division pulls the first primary medially to close the gap between the primaries and the secondaries. Because of ligamental connections between the primaries, the action affects most of the primaries, but especially the medial primaries. The anterior anconal part flexes the hand on the forearm. The palmar slip draws the primaries medially and tends to flex the hand; the latter action probably is unimportant.

Comparison.—Similar in the New World vultures except that in *Sarcoramphus* the posterior anconal fasciculus also inserts on the most lateral secondary. The muscle is largest in *Cathartes* and *Coragyps*. It is smallest in *Vultur*.

M. flexor metacarpi posterior is an especially interesting muscle. There is no muscle antagonistic to it in the action of the feathers. The primaries are attached to the metacarpus at an angle, that is, their distal ends are farther laterally than are the proximal ends. The feathers are held to the metacarpus by heavy fascia. The action of this muscle pulls the distal ends medially against the passive action of the fascia; upon relaxation

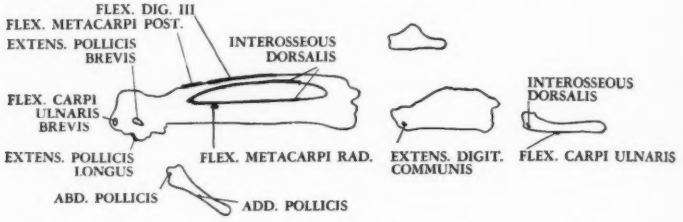


Fig. 13. *Coragyps atratus*. Palmar view of bones of tip of wing showing attachments of muscles, ×1/2.

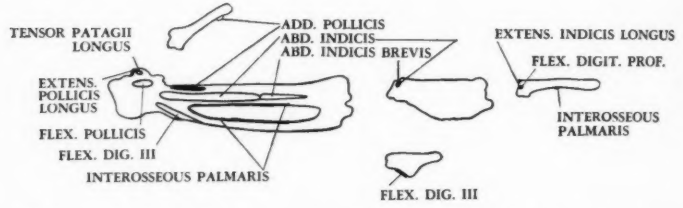


Fig. 14. *Coragyps atratus*. Anconal view of bones of tip of wing showing attachments of muscles, ×1/2.

of the muscle, the fascia which is elastic pulls the primaries into the position usually seen in specimens.

Medial movement of the distal ends of the primaries shortens and broadens the wing, which is important in the utilization of air currents as will be discussed later.

TABLE 18.—Ratios of volumes of individual muscles to the total volume of the wing muscles.

	Cathartes	*Coragyps*	*Gymnogyps*	*Vultur*	*Sarcoramphus*
pectoralis superficialis					
superficial layer	56.00	50.30	43.97	50.23	52.40
deep layer	4.40	3.82	9.22	7.30	4.28
supracoracoideus	4.40	6.50	5.14	7.30	5.79
coracobrachialis post.	1.10	1.07	1.16	1.12	0.93
latissimus dorsi	1.20	1.68	1.91	1.71	1.69
rhomboideus superficialis	0.80	0.97	1.24	0.98	1.64
rhomboideus profundus	0.80	1.00	1.13	0.74	0.86
coracobrachialis anterior	0.70	0.74	1.24	1.24	0.68
deltoideus minor	0.50	0.40	1.35	0.76	0.50
proscapulohumeralis	1.10	1.21	1.88	1.56	1.31
dorsalis scapulae	3.20	3.49	2.70	2.41	3.83
serratus posterior	1.10	1.00	1.43	1.13	1.26
subcoracoideus	0.50	0.23	—	—	0.28
proscapulohumeralis brevis	0.70	0.66	0.05	0.02	0.25
serratus profundus	0.38	0.47	0.57	0.36	0.39
serratus anterior	0.04	0.10	0.05	0.04	0.038
tensor patagii brevis and tensor patagii longus	1.60	1.84	1.16	1.38	1.46
biceps	3.50	3.15	3.19	3.27	3.78
deltoideus major	3.80	4.09	2.33	2.90	4.28
triceps-scapular head	3.10	3.28	3.54	3.64	3.91
int. and ext. heads	2.40	3.15	3.96	2.80	2.26
brachialis	0.31	0.47	0.92	0.48	0.39
extensor metacarpi radialis	1.10	1.71	1.50	1.06	1.03
extensor digitorum communis	0.31	0.30	0.25	0.26	0.25
supinator brevis	0.20	0.30	0.57	0.44	0.33
flexor metacarpi radialis	0.11	0.47	0.60	0.45	0.31
pronator brevis	0.80	0.81	0.81	0.60	0.78
pronator longus	1.10	1.71	1.50	1.02	1.11
extensor pollicis longus	0.50	0.60	0.71	0.51	0.43
anconeus	0.50	0.87	1.06	0.73	0.55
extensor indicis longus	0.13	0.27	0.29	0.11	0.17
flexor digitorum profundus	0.18	0.20	0.32	0.26	0.20
flexor carpi ulnaris	1.60	1.69	2.16	1.70	1.54
flexor carpi ulnaris brevis	0.40	0.40	0.35	0.24	0.239
abductor pollicis	0.08	0.03	0.07	0.05	0.063
adductor pollicis	0.07	0.03	0.05	0.05	0.05
flexor digiti III and flexor brevis digiti III	0.08	0.07	0.10	0.08	0.05
flexor metacarpi brevis	0.03	0.01	0.01	0.01	0.013
interosseus dorsalis	0.11	0.10	0.09	0.07	0.11
interosseus palmaris	0.08	0.07	0.12	0.08	0.08
extensor pollicis brevis	0.02	0.02	0.04	0.01	0.013
abductor indicis	0.13	0.10	0.19	0.24	0.151
abductor indicis brevis	—	0.03	—	—	—
flexor pollicis	0.07	0.02	0.04	0.02	0.033
flexor metacarpi posterior	0.38	0.37	0.29	0.15	0.30
dermo-tensor patagii	0.80	0.37	0.57	0.45	0.33
Total Per Cent	98.4	100.3	97.8	99.9	100.3

Table 19.—Synonymy of the Muscles of the Wing.

Shufeldt, 1890	Fürbringer, 1888	Gadow, 1890	Howell, 1937	Fisher
pectoralis major	pectoralis thoracicus	pectoralis thoracica	pectoralis superficialis	pectoralis superficialis
pectoralis secundus	supracoracoideus	supracoracoideus (subclavius in plates)	coracobrachialis	supracoracoideus
pectoralis tertius	coraco-brachialis internus s. posterior	coraco-brachialis posterior	coracobrachialis posterior	coracobrachialis posterior
latissimus dorsi	latissimus dorsi dermal components lat. dorsi metapat. lat. dorsi dorsi-cutaneus	same as Fürbringer	latissimus dorsi	latissimus dorsi
trapezius	rhomboideus superficialis	rhomboideus superficialis	rhomboideus superficialis	rhomboideus superficialis
rhomboideus	rhomboideus profundus	rhomboideus profundus	rhomboideus profundus	rhomboideus profundus
coraco-humeralis	coraco-brachialis externus s. anterior	coraco-brachialis anterior	coracobrachialis anterior	coracobrachialis anterior
scapulo-humeralis	deltoides minor	deltoideus minor	deltoideus deep-brevis	deltoideus minor
teres et infraspinatus	scapulo-humeralis posterior	scapuli-humeralis posterior	dorsalis scapulae	dorsalis scapulae

teres et infraspinatus	scapulo-humeralis posterior	scapuli-humeralis posterior	scapulae	scapulae

supraspinatus	scapulo-humeralis anterior	scapuli-humeralis anterior	proscapulo-humeralis	proscapulo-humeralis
subscapularis	subscapularis internus	subscapularis internus	subscapularis	subscapularis
coraco-brachialis	subcoracoideus	subcoracoideus	subcoracoideus	subcoracoideus
serratus magnus anticus	serrati superf. pars posterior	serrati superf. s. thoracici-scap. pars posterior	posterior serratus (part)	serratus posterior
dermo-ulnaris pt.	pars metapatag.	pars metapatag.	serratus metapatag.	serratus metapatag.
subclavius	sternocoracoideus	sternocoracoideus	sternocoracoideus	sternocoracoideus
teres minor	scapulo-humeralis anterior?	scapuli-humeralis anterior?	.....	proscapulo-humeralis brevis
levator scapulae	serratus profundus	serratus profundus	.....	serratus profundus
thoraco-scapularis	serrati superf. pars posterior	serrati superf. s. thoracici-scapularis	posterior serratus (pt.)	serratus posterior (deep layer)
serratus parvus anticus	serrati superficialis pars anterior	serrati superficialis s. thoracici-scapularis (pars anterior) [serratus minor of plate XXI]	anterior serratus	serratus anterior
tensor patagii brevis	deltoides propatagialis brevis	propatagialis deltoidei	deltoideus superf. layer?	tensor patagii brevis

Table 19.—Synonymy of the Muscles of the Wing—Continued.

Shufeldt, 1890	Fürbringer	Gadow, 1890	Howell, 1937	Fisher
tensor patagii longus	deltoides propatagialis longus	propatagialis deltoidei	.....	tensor patagii longus
dermo-tensor patagii	pectoralis propatagialis (pt.)	propatagialis pectoralis	deltoideus superf. layer?	dermo-tensor patagii
biceps	biceps brachii	biceps brachii	biceps	biceps
deltoid	deltoides major	deltoideus major	deltoideus (deep layer)	deltoideus major
triceps		triceps cubiti s. anconaeus	triceps	triceps
scapular head	anconaeus scapularis	scapuli-cubitalis	scapulotriceps	scapular head
external head	anconaeus humeralis	humero-cubitalis	humerotriceps	external head
internal head	anconaeus humeralis	humero-cubitalis	humerotriceps	internal head
brachialis anticus	brachialis inferior	brachialis inferior	brachialis	brachialis
extensor metacarpi radialis longior	extensor metacarpi radialis (pars longus and pars profundus)	extensor metacarpi radialis	.....	extensor metacarpi radialis pars anconalis pars palmaris
extensor digitorum communis	.....	extensor digitorum communis	.....	extensor digitorum communis
supinator brevis	.....	ectepicondylo-radialis (supinator on plates)	.....	supinator brevis

(supinator on plates)

flexor metacarpi radialis	extensor metacarpi ulnaris, no. 89	flexor metacarpi radialis
pronator brevis	entepicondylo-radiales, pronator sublimis	pronator brevis
pronator longus	entepicondylo-radialis, pronator profundus	pronator longus
extensor ossis metacarpi pollicis	extensor pollicis longus	extensor pollicis longus
anconeus	ectepicondylo-ulnaris	anconeus
extensor indicis longus	extensor indicis longus	extensor indicis longus
flexor digitorum sublimis	flexor digitorum sublimis	flexor digitorum sublimis
flexor digitorum profundus	flexor digitorum profundus	flexor digitorum profundus
flexor carpi ulnaris	flexor carpi ulnaris s. entepicondylo-carpalis	flexor carpi ulnaris
flexor carpi ulnaris brevior	ulni-metacarpalis ventralis	flexor carpi ulnaris brevis
extensor proprius pollicis	abductor pollicis	abductor pollicis
----------	flexor pollicis	flexor pollicis
----------	extensor pollicis brevis	extensor pollicis brevis
flexor brevis pollicis	adductor pollicis	adductor pollicis
flexor minimi digiti	flexor digiti III	flexor digiti III
flexor minimi digiti brevis	----------	flexor brevis digiti III
----------	----------	flexor metacarpi posterior
----------	abductor indicis	abductor indicis
----------	----------	abductor indicis brevis
abductor minimi digiti	----------	abductor digiti II
flexor metacarpi brevis	ulni-metacarpalis dorsalis	flexor metacarpi brevis
interosseus dorsalis	interosseus dorsalis	interosseus dorsalis
interosseus palmaris	interosseus palmaris	interosseus palmaris

Correlation of Differences in Myology with Differences in the Use of the Wing

In relation to the body weight the musculature of the wing is greatest in *Cathartes* and smallest in *Gymnogyps*. The ratios are: *Cathartes*, 52.3; *Sarcoramphus*, about 48 (exact weight unknown); *Coragyps*, 33.1; *Gymnogyps*, 24.7; in *Vultur* the ratio probably approximates the ratio of *Coragyps*, but no weight was available for the specimen of *Vultur*.

Ratios of the volume of the wing musculature to the length of the wing are: *Cathartes*, 47.6; *Coragyps*, 33.1; *Sarcoramphus*, 74.1; *Gymnogyps*, 88.0; *Vultur*, 124.0 Thus there is a correlation of the wing length and the relative development of the musculature; with increases in length the surface increases as a square, more or less, and this accounts in part at least for the increase in the muscles. However, relative breadth of the wing is an important factor. It has been demonstrated previously that the wing is widest in proportion to its length in *Coragyps* and *Sarcoramphus* and narrowest in *Cathartes*. The relative width in *Vultur* is appreciably less than in *Gymnogyps;* the ratio for these genera is closer to the ratio for *Cathartes* than to the ratio for *Coragyps*. Consequently, the muscles of the wing, in proportion to the length and width of the wing, are better developed in *Cathartes* than in *Coragyps* and better in *Vultur* than in *Gymnogyps*. *Sarcoramphus*, as regards the gross development of the wing-musculature in relation to wing-size is between the smaller vultures and the condors.

Considering body weight, wing length and wing width the musculature is best developed in *Cathartes;* it is next best developed in *Coragyps*. In *Vultur* the wing muscles are relatively larger than in *Gymnogyps* but somewhat smaller than in *Coragyps*. *Sarcoramphus* is again intermediate between the condors and smaller vultures. The larger muscles in *Cathartes* enable it to flap with greater ease than any other vulture. The laborious flapping flight of *Coragyps*, as compared to *Cathartes*, is correlated with smaller muscles. The condors are less able to flap than *Sarcoramphus* and the small vultures because they possess longer wings and relatively weaker musculature.

The discussion of wing musculature as a whole is significant, but relative development of individual muscles (table 18) and their location and configuration are more important in analyzing the potentialities of the musculature of the wing.

Muscles moving the scapula.—Movement of the scapula is much restricted in birds. In forms which flap, the shoulder must be held firmly to provide a stable foundation for the movement of the wing; yet there are movements along both the anteroposterior and dorsoventral axes. A shift forward of the shoulder means that the entire wing is moved anteriorly in relation to the center of gravity, which in turn increases the angle of incidence by raising the anterior end of the body. A shift posteriorly of the shoulder causes the reverse to occur.

By raising the scapula and shoulder complex the wings are elevated, which has the effect of lowering the center of gravity. A lower center of gravity of the body, in relation to the wings, provides for greater stability in soaring.

The muscles which move the scapula forward are the M. rhomboideus profundus and serratus profundus. The combined volumes of these muscles is relatively greatest in *Sarcoramphus* and *Gymnogyps;* it is smallest in *Cathartes* and *Vultur* (table 18). Since no significant differences in the attachments of these muscles were found among the cathartids, it must be concluded that forward movement of the scapula is easiest in the king vulture and the California condor.

Muscles tending to move the scapula posteriorly are M. rhomboideus superficialis, most of M. serratus posterior, and M. serratus anterior. The total relative volume in these muscles is: *Sarcoramphus,* 2.94; *Gymnogyps,* 2.72; *Vultur,* 2.15; *Coragyps,* 2.07; *Cathartes,* 1.94. The greater volume in *Sarcoramphus, Gymnogyps* and *Vultur* is largely a result of the additional development of the dermal components, M. serratus metapatagialis. Therefore these muscles show little variation in size among the New World vultures.

The scapula is pulled ventrally only by Mm. serratus posterior and serratus anterior. There are of course muscles attached to the lower edge of the scapula and extending to the humerus, but these do not affect the relative position of the scapula and the trunk. There is no significant variation in the relative size or in the attachments of Mm. serratus posterior and serratus anterior, except for the greater development of the dermal component in *Sarcoramphus, Gymnogyps* and *Vultur.*

The greatest bulk of the muscles attaching to the scapula (and furculum) is made up of the muscles which elevate the scapula and move it medially. These include Mm. rhomboideus superficialis, rhomboideus profundus and serratus profundus. They are relatively largest in *Gymnogyps* and smallest in *Sarcoramphus* and *Cathartes.* No significant differences in attachments were found.

The foregoing discussion of the muscles serving to move the shoulder, and especially the scapula, demonstrates that few differences are present among the cathartids. However, there are indications that the shoulder musculature is somewhat weaker in *Cathartes.* Because the scapula must be held firmly and must describe similar movements in both flapping and soaring birds no correlation with type of flight can be made.

Muscles moving the humerus.—The humerus may be elevated, depressed, extended, flexed and rotated. It is admitted that many or all of the muscles attached to the humerus may cause two or more of these movements, but in all cases synergistic muscles may act to eliminate these movements. Therefore, each muscle will be discussed in relation to each separate action it may cause.

Muscles which may elevate the humerus include Mm. supracoracoideus, deltoideus major, deltoideus minor, proscapulohumeralis, dorsalis scapulae, and the scapular head of M. triceps. Mm. proscapulohumeralis and dorsalis

scapulae insert on the proximal part of the bicipital crest and consequently have a power arm too short for much effective elevation of the humerus.

The volume of all muscles that may aid in raising the humerus constitutes 19.6 per cent of the total volume of the wing muscles in *Sarcoramphus,* 15.9 in *Coragyps,* 15.7 in *Vultur,* 14.6 in *Gymnogyps* and 12.3 per cent in *Cathartes.* If the volumes of the Mm. proscapulohumeralis and dorsalis scapulae, which function chiefly to raise the posterior edge of the wing, are omitted, the percentages are: *Sarcoramphus,* 14.5; *Vultur,* 11.7; *Coragyps,* 10.2; *Gymnogyps,* 10.0; *Cathartes,* 8.0. Considering only the relative volumes, elevation of the humerus is strongest in *Sarcoramphus* and weakest in *Cathartes.*

The short wing of *Coragyps* and *Sarcoramphus* as compared to *Cathartes* and the condors is a major factor increasing the power of the elevators of the humerus in the former.

M. supracoracoideus is more anteriorly situated in *Cathartes* than in *Gymnogyps* and *Vultur;* this increases the efficiency of the muscle by placing its longitudinal axis more nearly in the desired line of action and by decreasing the waste force exerted on the coracoid.

In *Cathartes* the power arms of M. deltoideus major and M. deltoideus minor are significantly shorter than in the other cathartids; this increases the speed of elevation but decreases the power of elevation.

As suggested previously, the insertion of M. dorsalis scapulae in *Coragyps* and *Sarcoramphus* is at the proximal end of the bicipital crest. In *Cathartes, Gymnogyps* and *Vultur* the insertion is on the middle of the length of the crest, which provides a longer power arm for raising the humerus.

Two other muscles which are in a position to aid in elevating the humerus are Mm. tensor patagii brevis and proscapulohumeralis brevis. Actually, they probably contribute little to this action, but they must be considered. M. tensor patagii brevis is largest in *Coragyps* and smallest in *Gymnogyps;* in *Cathartes* it is slightly smaller than in *Coragyps* and in *Sarcoramphus* and *Vultur* it is slightly larger than in *Gymnogyps.* M. proscapulohumeralis brevis is much larger in the small vultures than in the king vulture and the large condors.

Therefore, because the muscles raising the humerus in *Coragyps* are larger than in *Cathartes* the power available is greater and elevation is easier. Speed of elevation may be greater in *Cathartes* because of more proximal insertions of Mm. deltoideus, but there is no difference in the insertion of M. supracoracoideus which is the most powerful levator; and M. supracoracoideus is 50 per cent larger in *Coragyps* than in *Cathartes.*

Better development of the muscles raising the wing in *Coragyps,* as compared to *Cathartes,* is correlated with the greater speed of flapping exhibited by the black vulture.

In ability to raise the wing *Sarcoramphus* is nearer to the small vultures than to the condors.

Vultur can elevate the wing more easily than *Gymnogyps* because the levator muscles are better developed in the Andean condor. *Vultur* approaches the condition found in *Coragyps*.

Muscles which may depress the humerus and consequently the wing are: M. pectoralis superficialis, coracobrachialis posterior, coracobrachialis anterior and subcoracoideus. M. pectoralis superficialis is the main muscle, however; the others function primarily in tilting the humerus.

The combined volume of all muscles which may aid in depressing the wing constitutes 62.7 per cent of the wing musculature in *Cathartes*, 59.9 per cent in *Vultur*, 58.6 per cent in *Sarcoramphus*, 56.2 per cent in *Coragyps* and 53.2 in *Gymnogyps*. M. pectoralis superficialis is 60.4 per cent of the total wing musculature in *Cathartes*, 57.5 in *Vultur*, 56.7 in *Sarcoramphus*, 54.1 in *Coragyps*, and 53.2 in *Gymnogyps*.

Wing length and body weight are important in the discussion of M. pectoralis superficialis. The ratios of its volume to the wing length are: *Vultur*, 62.3; *Gymnogyps*, 60.9; *Sarcoramphus*, 42.3; *Cathartes*, 26.4; *Coragyps*, 17.9. Ratios of volume to body weight are: *Cathartes*, 29.3; *Sarcoramphus*, 27.1? and *Vultur*, 18.0? (no weights available); *Coragyps*, 16.6; *Gymnogyps*, 11.3.

Previous workers have reported a positive correlation between the development of M. pectoralis superficialis and the ability to flap. I fail to see any such simple correlation.

In the discussion of the bones of the wing it was pointed out that the humerus is shorter than the trunk in *Coragyps*, slightly longer than the trunk in *Sarcoramphus* and *Vultur* and approximately one-fifth longer than the trunk in *Gymnogyps* and *Cathartes*. Further, it was demonstrated that the long wing of *Cathartes* is primarily a result of increased length distal to the humerus. In *Vultur* and *Gymnogyps* the long wing results from a more nearly equal increase in all segments, but chiefly in the distal parts.

Because of this lengthening of the distal wing bones in the turkey vulture, as compared to *Coragyps*, the power arm for M. pectoralis superficialis is much shorter in relation to the work arm. To a lesser extent this is true in the large condors.

Development of certain structural features of M. pectoralis superficialis is correlated with the type of flight. In soaring the main function of the muscle is to hold the wing down against the upward force of air beneath the wing; because of a longer power arm and because its longitudinal axis lies more nearly in the line of pull, the posterior part is the important element in this action. Consequently in *Vultur* and *Gymnogyps* the posterior part of the muscle is very well developed; the anterior part is thin and partly tendinous. In *Vultur* the middle third of the superficial layer overlying the deep layer is entirely tendinous. The tendinous condition of the anterior part of the superficial layer limits the amount of contraction possible there; the thick, fleshy posterior part does most of the work, but the anterior tendinous section

eases the strain on the muscles when the wings are held extended for long periods in soaring. It would be impossible for the longer posterior part to be tendinous since this would seriously restrict the range of movements of the distal end of the humerus.

To move the humerus anteriorly the following muscles may act: pectoralis superficialis (anterior part), anterior fleshy part of M. supracoracoideus, coracobrachialis anterior and biceps. The volume of these muscles exclusive of M. pectoralis superficialis and M. supracoracoideus is 4.51 per cent of the wing musculature in *Vultur,* 4.46 per cent in *Sarcoramphus,* 4.43 in *Gymnogyps,* 4.20 in *Cathartes* and 3.89 in *Coragyps.*

The anterior part of the superficial layer of M. pectoralis superficialis, which serves to move the humerus anteriorly, is much weaker in the condors than in the small vultures. *Coragyps* and *Sarcoramphus* are the only forms possessing a well developed anterodorsal part of the deep layer of M. pectoralis superficialis; this increases the effective anterior force on the humerus.

The fleshy anterior part of M. supracoracoideus, which arises from the furculum and the membrane between the furculum and the coracoid is smallest in *Coragyps;* it is equally developed in the other genera.

The better development anteriorly of M. pectoralis superficialis in *Coragyps,* as compared to *Cathartes,* probably more than offsets the difference in relative volumes of the other muscles between these two forms. The larger size of this part in *Sarcoramphus* and the turkey and black vultures, as compared to the condors, increases the effective anteriorly directed pull and largely offsets the better development of the other muscles which move the humerus anteriorly in the California and Andean condors.

From the above discussion one may see that there is little difference among cathartids in the ability to move the humerus anteriorly.

The following muscles may draw the humerus posteriorly: Mm. pectoralis superficialis, latissimus dorsi, proscapulohumeralis, dorsalis scapulae, subcoracoideus, proscapulohumeralis brevis, deltoideus major, deltoideus minor, and the scapular head of M. triceps. Exclusive of M. pectoralis superficialis, the relative volumes of these muscles are: *Sarcoramphus,* 16.05; *Coragyps,* 15.0; *Cathartes,* 14.1; *Gymnogyps,* 13.8; *Vultur,* 13.0. If relative volume only is used as an index, ability to flex the humerus posteriorly is greatest in *Sarcoramphus* and *Coragyps* and may be correlated with the ability to flap.

It is not practical to use the size of M. pectoralis superficialis as an index to the ability to move the wing posteriorly, although on the down stroke this is the only muscle which could flex the humerus without opposing the downward movement of the wing.

If the wing length is considered, the effect of the difference in relative volume between *Coragyps* and *Cathartes* is augmented by the much longer work arm in the turkey vulture.

Important differences in attachments of the muscles flexing the humerus posteriorly are few and occur only in M. deltoideus major and the scapular head of M. triceps. In *Vultur, Sarcoramphus* and *Gymnogyps* there is an additional tendon of origin for M. deltoideus major. This tendon runs to the middle of the dorsolateral edge of the scapula and thereby provides a strong, more posterior source of origin. The more posterior origin causes the muscle to lie more nearly in the direction of force to pull the humerus posteriorly.

The scapular head of M. triceps in *Vultur* and *Gymnogyps* is attached by a wide tendon on the distal edge of M. latissimus dorsi.

As regards ability to pull the humerus posteriorly, the cathartid genera, listed in order of decreasing ability, are: *Coragyps, Sarcoramphus, Cathartes* and *Gymnogyps* and *Vultur*. Probably this is also the order of decreasing use of flapping flight (no observations on *Sarcoramphus*).

Elevation and depression of the anterior edge of the wing to change the angle of incidence of the wing are important in all types of flight. In soaring birds the variations in the angle are relatively slight. In flapping types the entire wing may be tilted. For example, to give forward propulsion on the downstroke the anconal surface of the wing may be rotated so far forward that its anteroposterior axis is almost vertical. For the most part this extreme rotation occurs only in swift, narrow-winged types. In birds with a long broad wing only the distal parts of the wing are rotated.

Muscles functioning to increase the angle of incidence of the wing may be divided into two groups those that raise the anterior edge of the wing and those that depress the posterior edge.

Mm. coracobrachialis posterior, latissimus dorsi, deltoideus major and deltoideus minor function to raise the anterior edge of the upper arm part of the wing. These muscles constitute 7.4 per cent of the wing muscles in *Sarcoramphus*, 7.24 per cent in *Coragyps*, 6.75 per cent in *Gymnogyps*, 6.60 per cent in *Cathartes* and 6.49 per cent in *Vultur*. Inclusion here of the entire M. latissimus dorsi unduly increases the relative volumes in the condors; two additional dermal components in these birds increase the volume of the muscle.

Muscles which increase the angle of incidence of the upper arm by depressing the posterior edge of the upper arm are the coracobrachialis posterior and subcoracoideus. Both these muscles are better developed in *Coragyps* and *Cathartes* than in *Sarcoramphus, Gymnogyps* and *Vultur*. The ventral part of M. subcoracoideus, which is the important part in depressing the posterior edge of the wing, is absent in *Vultur* and *Gymnogyps*. In addition, in the condors M. subcoracoideus is inseparably fused to M. proscapulohumeralis which acts to *raise* the posterior edge of the wing.

It must be concluded that *Coragyps* possesses the best mechanism for increasing the angle of incidence by raising the anterior edge of the upper arm. *Sarcoramphus* and *Cathartes* are next best adapted. The condors possess little ability to elevate the anterior edge of the humerus.

Depression of the anterior edge of the upper arm is accomplished by M. pectoralis superficialis (superficial layer chiefly). Elevation of the posterior edge of the wing is brought about by Mm. proscapulohumeralis and dorsalis scapulae.

The relative volume of M. pectoralis superficialis cannot be used as an index to the ability to depress the anterior edge of the wing because its chief function and major development obviously are for depression of the entire wing. The combined volumes of M. proscapulohumeralis and M. dorsalis scapulae are 5.14 per cent of the wing musculature in *Sarcoramphus*, 4.70 in *Coragyps*, 4.58 in *Gymnogyps*, 4.30 in *Cathartes* and 3.97 per cent in *Vultur*; the volumes in *Gymnogyps* and *Vultur* are not reliable indices because they include M. subcoracoideus which is not effective in raising the posterior edge of the upper arm.

Sarcoramphus and *Coragyps* are best adapted to depress the anterior edge of the proximal part of the wing as necessary in flapping flight. *Vultur* and *Gymnogyps* are least adapted in this regard. As indicated earlier, ability to rotate the proximal part of the wing is usually correlated with ability to flap. This appears to be the case with *Coragyps* and *Cathartes*, both of which flap more than do *Gymnogyps* and *Vultur*.

Muscles moving the forearm.—Flexors of the forearm include Mm. tensor patagii longus, tensor patagii brevis, dermo-tensor patagii, biceps, brachialis, extensor metacarpi radialis, extensor digitorum communis, supinator brevis, flexor metacarpi radialis, pronator longus, pronator brevis, anconeus and flexor carpi ulnaris. None of these muscles acts simply as a flexor; the one-joint group (brachialis, supinator, pronators and anconeus) is simplest in its action.

The aforementioned muscles, all of which *may* aid in flexing the forearm, equal 14.3 per cent of the wing muscles in *Gymnogyps*, 13.5 in *Coragyps*, 11.9 in *Cathartes* and *Sarcoramphus* and 11.7 in *Vultur*. Because the functions of these muscles are so varied these ratios may not be true indices of ability to flex the forearm.

The relative volume of M. biceps, M. tensor patagii brevis and M. brachialis is approximately the same among the cathartids. Considering only the volume of the one-joint group, *Gymnogyps* and *Coragyps* exhibit the best ability to flex the forearm.

However, neither the total relative volume of muscles which flex the forearm nor relative volumes of selected muscles provide reliable criteria, if used alone. Differences in position and manner of attachment must be considered.

Coragyps and *Cathartes* have a much longer power arm for the action of M. biceps than do *Gymnogyps* and *Vultur;* it is longer in *Sarcoramphus* than in the condors. The power arm is significantly longer in *Coragyps* than in *Cathartes*.

M. supinator brevis is limited to the proximal third of the forearm in the turkey vulture, the king vulture, the California and Andean condors. Since

the muscle in *Coragyps* extends distally almost to the middle of the length of the forearm there is a longer power arm in the black vulture.

The power arm of M. pronator brevis is longest in *Coragyps* and next longest in *Cathartes*.

M. anconeus possesses a power arm that is longest in *Coragyps* (53 per cent of ulnar length). In *Sarcoramphus* it is 49.5; in *Cathartes* it is 47.4; in *Vultur* and *Gymnogyps* it is 43 per cent of the ulnar length.

Because the muscles flexing the forearm are longer and have longer power arms in *Coragyps* than in *Cathartes*, it must be concluded that *Coragyps* is better adapted for this particular movement. *Cathartes* and *Sarcoramphus* can certainly flex the forearm more easily than *Vultur*. Although the muscles are larger in *Gymnogyps* than in *Cathartes*, I think the longer power arms of Mm. biceps, pronator brevis and anconeus in *Cathartes* more than offset the difference in the development of the muscles.

The ability to flex the forearm is correlated with the ability to flap the wings. The series of cathartids listed in order of decreasing use of flapping is *Coragyps* (*Sarcoramphus?*), *Cathartes*, and *Gymnogyps* and *Vultur*. The series is the same for decreasing ability to flex the forearm.

M. triceps is the only muscle in a position to extend the forearm. Except for the scapular head which flexes and elevates the humerus while extending the forearm, the entire muscle functions for extension. M. triceps is relatively larger in *Gymnogyps*, significantly smaller in *Coragyps*, *Sarcoramphus* and *Vultur* and the smallest in *Cathartes*.

In the condors the scapular head has a more distal insertion which provides a longer power arm than in the turkey, king and black vultures. The larger size of the muscles and the longer power arm furnish more power to extend the forearm in *Gymnogyps* and *Vultur*. The wing may be maintained in the extended position for long periods as in soaring with less effort on the part of the muscles.

The proximal insertion in *Coragyps* and *Cathartes* provides greater speed of extension which is necessary in flapping flight, but the smaller muscle in the turkey vulture, as compared to the black vulture, reduces the power available for extension.

There is no muscle which functions solely to elevate or to depress the forearm. However, when the forearm is completely extended, Mm. anconeus, flexor metacarpi radialis, extensor digitorum communis and supinator brevis may raise the forearm. It is of course assumed that the function of flexion, extension and supination, usually performed by these muscles, is prevented by the action of antagonistic and synergistic muscles. Under similar conditions the forearm may be slightly depressed by Mm. pronator longus, pronator brevis, flexor carpi ulnaris, flexor carpi ulnaris brevis, flexor digitorum profundus and brachialis.

The total volume of the muscles which may raise the forearm under the foregoing conditions is 2.13 per cent of the total wing musculature in *Gymnogyps*, 1.67 per cent in *Coragyps* and *Vultur*, 1.44 in *Sarcoramphus*, and 1.12 in *Cathartes*. Longer power arms for the action of Mm. anconeus and supinator brevis in *Coragyps*, as compared to the other genera, increase the power of levation in the black vulture. Similarly, longer power arms for these muscles in *Cathartes*, as compared to the condors, increases the power to raise the forearm. Therefore, considering both the development of the muscles and their power arms it may be stated that *Coragyps* can raise the forearm more easily than can *Vultur*. However, there is apparently no correlation between the ability to raise the forearm and the use of a particular mode of flight, that is, flapping or soaring.

Ability to depress the forearm shows exactly the same trends as ability to raise the forearm. However the muscles tending to depress the forearm are much larger than their antagonists in this function; this is a result of the need to hold the wing down against the upward force of the air.

M. brachialis and M. supinator brevis raise the anterior edge of the middle segment of the wing. Since these muscles exhibit no differences in attachment among the New World vultures, their combined volume is a reliable index to the power to raise the anterior edge of the forearm. In *Gymnogyps* they make up 1.49 per cent of the total volume of the muscles of the wing; in *Vultur* they constitute 0.92 per cent, in *Sarcoramphus*, 0.72, in *Coragyps*, 0.57, and in *Cathartes*, 0.51 per cent. Thus ability to raise the anterior edge of the forearm to increase the angle of incidence of the wing is roughly correlated with the ability to soar.

Mm. pronator longus, pronator brevis and anconeus function to depress the leading edge of the forearm. The relative size of these muscles is 50 per cent greater in *Gymnogyps* than in the other genera. There are no significant differences in the attachments among the cathartids. However, no correlation with type of flight is possible because the upward force of air beneath the distal tips of the secondaries in all cases tends to depress the anterior edge of the forearm without the intervention of muscular action.

Muscles moving the metacarpus.—These muscles may be discussed in five groups, according to their action on the metacarpus,—extensors, flexors, levators, depressors and rotators.

The muscles which extend the metacarpus are: tensor patagii longus, tensor patagii brevis, extensor metacarpi radialis, extensor digitorum communis, extensor pollicis longus, extensor indicis longus and flexor digitorum sublimis (anterior tendon of flexor carpi ulnaris). These muscles are best developed in *Coragyps* (4.72 per cent of wing muscles); the ratio is 3.91 in *Gymnogyps*, 3.64 in *Cathartes*, 3.32 in *Vultur* and 3.17 in *Sarcoramphus*.

The only significant difference in the extensors of the metacarpus among the cathartids is that M. tensor patagii longus inserts farther distally on the extensor process in *Cathartes*, *Gymnogyps* and *Vultur*. The longer power

arm thus provided in these forms increases the effectiveness of the muscle. The shorter power arm and larger muscle in *Coragyps* forms a better mechanism for the quick, powerful extension necessary in flapping flight; to a lesser extent this is also true in *Sarcoramphus*.

Another factor enters into the discussion of the extension of the hand. The anterior superficial tendon of M. flexor carpi ulnaris (M. flexor digitorum sublimis) may act as an automatic extensor of the hand when the forearm is extended. The tendon is larger in *Cathartes, Gymnogyps* and *Vultur* than in *Sarcoramphus* and *Coragyps*. Its development is correlated with the ability to hold the wing extended for long periods; it eases the work of the extensor muscles.

The metacarpus is flexed by Mm. flexor metacarpi radialis, flexor digitorum profundus, the posterior part of M. flexor carpi ulnaris, flexor metacarpi brevis and flexor metacarpi posterior. These muscles make up 3.39 per cent of the volume of the muscles of the wing in *Gymnogyps*, 2.74 per cent in *Coragyps*, 2.57 in *Vultur*, and 2.30 per cent in *Cathartes* and *Sarcoramphus*. These figures of relative development show no correlation with the pattern of flight.

However, if wing length is considered, *Coragyps* with its short wing probably possesses the best mechanism for flexion of the hand. The relatively long wing in *Cathartes*, as compared to all the other genera, reduces the efficiency of flexion; this fact together with the lesser development of the muscles makes flexion most difficult in the turkey vulture.

The joint between the ulna and the metacarpus is chiefly a hinge joint and permits only restricted independent levation and depression of the metacarpus. More rotatory movement is possible.

Only one muscle, M. flexor metacarpi brevis, functions to raise the metacarpus, and its action is negligible. When the wing is fully extended, Mm. extensor pollicis longus, flexor metacarpi radialis, extensor digitorum communis, and extensor indicis longus may raise the manus slightly, but it is impossible to calculate their possible effect.

The strong tendons extending from the distal end of the radius to the middle of the length of the palmar surfaces of metacarpals II and III and to the pisiform process (fig. 2) serve to hold the hand down against the pressure of air beneath the primaries. They are equally developed in the New World vultures.

There is no muscle whose chief function is depression of the metacarpus. The tendons discussed above restrict its upward movement, and when the hand is fully extended, Mm. flexor carpi ulnaris and flexor digitorum profundus may slightly depress the metacarpus.

M. flexor carpi ulnaris brevis is the only muscle in a position to tilt the manus as a unit; it depresses the anterior edge and thus decreases the angle of incidence. The muscle is equally developed in *Cathartes, Coragyps* and *Gymnogyps*; it is much smaller in *Sarcoramphus* and *Vultur*.

Muscles moving digit I.—The alula is extended by Mm. abductor pollicis and extensor pollicis brevis. The combined volumes of these two muscles is roughly twice as large in *Cathartes* and *Gymnogyps* as in *Sarcoramphus, Coragyps* and *Vultur.*

In *Gymnogyps* the insertion of M. abductor pollicis is on the distal end of the digit; in the other genera it is on the middle of the length of bone. Consequently, *Gymnogyps* possesses the best mechanism for extending the alula and separating it from the rest of the wing. The importance of this action has been discussed previously (p. 551).

Mm. extensor digitorum communis, adductor pollicis and flexor pollicis move the alula posteriorly and hold it next to the anterior edge of the rest of the wing; this action streamlines the wing and increases the speed of soaring flight.

These muscles are best developed in *Cathartes;* they are somewhat larger in *Coragyps* and *Sarcoramphus* than in *Gymnogyps* and *Vultur.*

The origin of M. adductor pollicis is farther distal in *Cathartes, Gymnogyps, Sarcoramphus* and *Vultur* than in *Coragyps.* The more distal origin decreases the force wasted in end thrust against metacarpal I and thus increases the force effective in adducting the alula. Therefore, the genera in order of decreasing ability to flex the pollex are: *Cathartes, Gymnogyps, Vultur, Sarcoramphus* and *Coragyps.* Ability to flex the pollex is correlated with soaring ability.

The alula is held down and depressed by Mm. abductor pollicis, adductor pollicis and flexor pollicis. The muscles are by far the best developed in *Cathartes;* they are stronger, however, in *Gymnogyps* and *Vultur* than in *Sarcoramphus* and *Coragyps.*

More distal insertion of M. abductor pollicis in *Gymnogyps* as compared to the other genera increases the effectiveness of the muscle. In *Coragyps* the origin of M. adductor pollicis is more proximally situated than in the turkey and king vultures and the California and Andean condors. In *Vultur, Sarcoramphus* and *Gymnogyps* the insertion of M. adductor pollicis is on the bases of the alular feathers; this more posterior insertion increases the vector of force pulling the alula toward the palmar side of the wing.

Considering the relative volumes and the attachment of the muscles depression of the alula is strongest in *Cathartes* and slightly weaker in *Gymnogyps* and *Vultur.* The action is weakest in *Sarcoramphus* and *Coragyps.* Ability to depress the pollex is apparently correlated with soaring ability.

M. extensor pollicis brevis raises the thumb. It is best developed in *Gymnogyps* and is weakest in *Sarcoramphus* and *Vultur;* it is developed equally in *Cathartes* and *Coragyps.*

Muscles moving digits II and III.—Strong ligamental attachment between digit III and phalanx 1 of digit II precludes independent movement of the digits.

Mm. extensor digitorum communis, extensor indicis longus, flexor digitorum profundus, interosseus dorsalis, abductor indicis and abductor indicis brevis extend digits II and III. They constitute 1.12 per cent of the volume of the wing muscles in *Gymnogyps*, 1.00 per cent in *Coragyps*, 0.95 in *Vultur*, 0.88 in *Sarcoramphus*, and 0.86 per cent in *Cathartes*. Because of differences in muscular attachments these relative volumes are not reliable indices of ability to extend the digits.

In all the cathartids, except *Coragyps* and *Sarcoramphus*, the insertion of M. flexor digitorum profundus is on the anteropalmar corner of the base of phalanx 2 of digit II; in *Coragyps* and *Sarcoramphus* the insertion is on the palmar surface of the base of the phalanx. Consequently in these two vultures, M. flexor digitorum profundus is better adapted for depression than for extension of the index digit; in fact, the muscle probably accomplishes little extension in the black and king vultures. If the relative volume of M. flexor digitorum profundus is subtracted from the total volume of muscles operating to extend digit II in *Coragyps* and *Sarcoramphus*, these vultures possess the smallest volume of extensor muscles for digit II. Thus the development of these muscles is correlated with ability to soar.

In *Gymnogyps*, M. abductor indicis inserts on the anteroanconal corner of the base of phalanx 1, digit II, rather than on the anteropalmar corner as in the other cathartids. Since the muscle is situated on the palmar surface of the hand, its passage anconally across the anterior face of the hand, as in the California condor, increases its effectiveness as an extensor. At the same time this insertion increases the ability to depress the anterior edge of the digit.

Digits II and III are flexed by Mm. flexor digiti III, flexor brevis digiti III and interosseus palmaris. These muscles are best developed in *Gymnogyps* and are least developed in *Sarcoramphus* and *Coragyps;* they are intermediate in size in *Cathartes* and *Vultur*. Since there are no differences in the attachments of the muscles, relative development is an index to ability to flex the digits, which ability is apparently best in soaring birds.

Mm. flexor metacarpi brevis, interosseus dorsalis and interosseus palmaris aid in elevating digits II and III. These muscles are strongest, as indicated by their relative volumes, in *Gymnogyps* and *Vultur;* they are weakest in *Coragyps*.

M. flexor digitorum profundus, M. abductor indicis and M. abductor indicis brevis serve to depress digits II and III and to hold them down against the upward press of air. They are significantly smaller in the small vultures than in the large condors.

Use of the Tail

The twelve rectrices in all cathartids are intimately and strongly interconnected basally by fibrous bands. These bands are especially large between rectrices 1, 2 and 3 on either side. In addition, rectrix 1 is immovably attached to the pygostyle by ligaments and fascia; this rectrix is thus dependent for its movements upon the movements of the pygostyle. The other rectrices however may be moved independently of the pygostyle. A heavy layer of fascia

just beneath the skin overlies the bases of all the tail feathers and the pygostyle.

The tail in the vultures is put to much more delicate use than in most birds. In the cathartids, except possibly *Coragyps*, its main function is in soaring flight. All who have observed soaring vultures have noticed the fine adjustments which the tail undergoes—tilting of one or both sides, slight depression, and abduction and adduction of the rectrices. These are especially evident on warm, calm days when every advantage must be taken of air currents. In these movements the tail functions mainly as a lateral stabilizer or balancer and as a rudder to control the direction of flight.

Another major use of the tail is as an airbrake when the bird comes in for a landing. As the body assumes a more vertical position, the head, neck and wings are extended ventrally and anteriorly, the legs are extended to touch the perch, and the tail is strongly depressed. This use of the tail is of course not limited to the Cathartidae.

In vultures the maximum movements of the tail are seen in preening. In preening it is often tilted at right angles to its more usual horizontal plane. Each time the bill is moved back to the oil gland the tail is pulled laterally. In wing and tail stretching when the bird is perched, the rectrices may be abducted so completely that the axes of the outer rectrices are in line. When moving on the ground or flex-gliding in the air, the tail may be "tented," that is, the medial feathers are held higher than the lateral rectrices.

It has not been possible to observe *Vultur* and *Sarcoramphus*, and I have found no published accounts of their habits of locomotion. Fortunately, Carl Koford has made available to me his extensive and detailed notes on the California condor. The habits of *Coragyps* and *Cathartes* have received some attention in published papers, and Mr. E. A. McIlhenny has kindly supplied observations on the use of the tail in *Coragyps*.

Without doubt the tail movements of *Gymnogyps* in flight are much more subtle and precise than in *Cathartes* and *Coragyps*. Koford has not observed *Gymnogyps* using the tail as a braking organ. In fact he believes the tail is seldom depressed, and Finley's (1923:177) photograph of a condor alighting shows the tail held almost horizontally. The California condor when perched exhibits all the varied caudal movements described above.

In *Coragyps* the tail movements in flight are greater and not nearly so well controlled. Its rectrices are relatively shorter and consequently of less use as a balancing and directing mechanism. Coarse and irregular movements of the tail are perhaps more permissible in a bird such as *Coragyps* which may depend upon flapping flight to maintain speed, balance and direction. Seldom does *Coragyps* abduct the rectrices to the extent seen in *Gymnogyps*. However, its tail is more elevated when walking. "Tenting" of the tail is most obvious in *Coragyps*, but this is infrequently seen in flight. In both the black and the turkey vulture the tail is used as a brake, but it seems to be more extensively used in this fashion by the former.

In regard to tail movement and use, the turkey vulture may be said to be

intermediate between the black vulture and the California condor. I have observed that the tail in *Cathartes* is capable of the motions described for *Gymnogyps* but that certain of these are less frequently employed. For example, I have seen complete abduction of the rectrices only a very few times; the tail, even in flight, is not as expanded as in *Gymnogyps*. However, in flight the tail movements more closely resemble those of the condor than those of the black vulture. Tail "tenting" is more infrequent than in *Coragyps*, and as a rule, on the ground, the tail is not elevated as high as in the latter bird.

Victor Coles (MS) has observed molting turkey vultures in which the tail feathers were almost completely gone—some molted out and the others broken. He could see no difference in their ability to soar along ridges where air currents were plentiful. Once in attempting to collect a turkey vulture I shot away all but one of the rectrices. The next day before it was collected I watched it for some time soaring along the lee side of a limestone cliff. It had no difficulty there, but when it moved out over a valley where the wind was strong it was evident that maintenance of balance was arduous without the stabilizing tail surface.

Walking is accompanied by lateral movements of the tail. When a leg is moved forward, the tail moves toward that side. This gives the impression of a waddling gait. Even though *Coragyps* actually waddles less in walking than *Gymnogyps* if leg movements only are considered, the lateral movements of the tail are more pronounced. *Cathartes* in turn shows more tail movement than the California condor, but it has a more straddled gait than does the black vulture.

Bones of the Tail

COCCYGEAL VERTEBRAE

Measurements of the articulated length of the coccygeal vertebrae, exclusive of the pygostyle, are incomplete as it was impossible to find a complete series for *Astur* and *Gymnogyps* (table 21). Comparison of this length with body and synsacral lengths (table 20) reveals that in the cathartids it is significantly less than in the Accipitridae. Of the Cathartidae, *Vultur* has perhaps the greatest length. Correlated with its short rectrices *Coragyps* has a short vertebral length.

TABLE 20.—Ratios Involving the Coccygeal Vertebrae and Pygostyle.

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Sarcoramphus	Vultur
Coccygeal vertebral length: trunk	31.3	—	30.7	31.8	25.2	21.9	24.2	25.7
Coccygeal vertebral length: synsacrum	42.1	—	42.2	42.8	26.0	26.5	27.3	31.2
Pygostyle length: trunk length	19.6	19.9	18.9	18.5	20.9	14.3	17.5	17.8
Pygostyle length: synsacrum	26.4	26.9	26.0	24.9	21.6	17.2	19.7	21.6
Width: length of pygostyle crest	34.4	39.5	34.0	39.7	44.0	40.3	46.0	37.9
Thickness: length of pygostyle crest	29.5	27.0	21.3	26.4	14.8	15.2	14.0	8.8

No important differences were noted in the structure of the free caudal vertebrae in the cathartids. Not only do the accipitrids have a longer coccyx but there are more free vertebrae (7, compared to 5 or 6 in the cathartids), and the transverse and neural processes are longer. The articulations in the hawks are stronger as manifested by the greater width and depth of the facets. At its proximal end the pygostyle is narrower and much thinner in the vultures. In the accipitrids, wide distinct flanges are present on the ventral edges lateral to the haemal canal. Muscles inserting on these flanges possess greater leverage for powerful, rapid tiltings of the tail. At the proximal end of the accipitrid pygostyle just anterior and ventral to the haemal canal is a well developed protuberance for the insertion of the depressor muscles. Of the cathartids this is best developed in *Sarcoramphus* and *Cathartes*. Levator muscle attachments are not visible on most cathartid pygostyles. Giebel (1855:26) found seven caudal vertebrae in both *Cathartes* and *Sarcoramphus*, but it is not known whether all these were free vertebrae. Shufeldt (1909:25) records six coccygeal vertebrae, exclusive of the pygostyle, in *Vultur* and *Sarcoramphus*, and five in *Coragyps* and *Cathartes*. In table 21 the number of coccygeal vertebrae in each genus is given.

My average measurements of the pygostyle and the ratios derived from them are not reliable because of the paucity of available pygostyles in certain genera, namely *Gymnogyps*, *Vultur* and *Sarcoramphus*, and because of the extensive individual variation as shown for example by the seven pygostyles of *Cathartes*. In a general sort of way the data indicate a shortened pygostyle in the vultures, except *Cathartes*. This shortening is especially evident in *Coragyps*. The crest is somewhat wider and is much thinner than in the accipitrids.

For illustration (plate 8) I attempted to use the most characteristic of the pygostyles but found it impossible to demonstrate all the features with only a single example of each genus. The pygostyle is seemingly very plastic somatically and is subjected to various modifying influences. Thus in many respects the phylogenetic differences in the pygostyles of the hawks and vultures are overshadowed and covered by modifications occasioned by similar use of the bone during the life time of the individual. Shufeldt (1909:29) attempts to delineate the various pygostyles. Comparison of these drawings with plate 8 in this paper demonstrates the variability of the pygostyle.

TABLE 21.—Average Measurements of Coccygeal Vertebrae and Pygostyle.

	Number vertebrae	Length vertebrae	Length pygostyle from facet	Width pygostyle crest	Length pygostyle crest
Accipiter	7	26.3 (4)	16.5 (4)	6.3 (4)	18.3 (4)
Astur	–	—	20.9 (1)	9.8 (1)	24.8 (1)
Aquila	7	54.4 (5)	33.6 (3)	13.9 (3)	40.9 (3)
Buteo	7	34.7 (4)	20.2 (3)	9.5 (3)	23.9 (3)
Cathartes	5 or 6	31.2 (5)	25.9 (5)	13.1 (7)	29.8 (5)
Coragyps	6 or 5	30.7 (4)	20.0 (3)	10.6 (3)	26.3 (3)
Sarcoramphus	5 or 6	38.5 (1)	27.8 (1)	15.8 (1)	34.3 (1)
Vultur	5 or 6	65.6 (2)	45.3 (2)	21.5 (2)	56.8 (2)

The pygostyle and the other free caudal vertebrae in the genera studied perform similar functions but at different rates of speed. In *Astur* and *Accipiter* the tail is used extensively for changing the direction of flight in the quick dash to capture the dodging prey. In the vultures the tail functions in a much more deliberate manner and limited scope as a directional organ and as a means of regulating the supporting surface. It is seldom that one sees a vulture in the air moving the tail as rapidly or as extensively as do certain hawks. In the former the movements are small, delicate tiltings or depressions to adjust the tail surface to the air currents.

Muscles of the Tail

Most of the tail muscles are composed of two or more parts, and these parts may have several tendons corresponding to the fasciculi of the muscle. It is this subdivision of muscles that makes possible the exact and minute maneuvering of the tail which is necessary in soaring flight.

Marshall (1872), Shufeldt (1890), Gadow (1891), Porta (1909), du Toit (1913) and Burt (1930) are the only modern workers who have considered the morphology of the tail. The work of Shufeldt on the raven is the most complete. Therefore, I have in most cases followed his system of nomenclature which is simpler than the multinomial system in Gadow's monograph.

MM. ADDUCTOR RECTRICUM

In these vultures the Mm. adductor rectricum (du Toit, 1913, plate 12) or the small dermal muscles just beneath the fascia between the bases of the rectrices are usually well developed, especially on the ventral surface. However, the muscles in the chicken always originate from the pygostyle and pass laterally to rectrix 6, giving off branches to rectrices 2, 3, 4, and 5. In the cathartids the muscle originating from the pygostyle inserts only on the median surface of rectrix 1; the muscle originating from the lateral surface of rectrix 1 inserts on the median surface of rectrix 2, and so on. In *Gymnogyps* they are widest (1.0 to 1.5 cm.) between rectrices 4 and 5 and 5 and 6. In the other genera they are smaller and are best developed between the inner three rectrices on each side. *Coragyps* has few fleshy fibers between the rectrices, but strong elastic bands of fascia are present.

Innervation of these muscles is from the last spinal nerve. Their function is adduction of the rectrices.

M. LEVATOR COCCYGIS

Description.—The muscle consists of three parts lying side by side, but overlapping each other (fig. 15). The three fasciculi are correlated with the origin from three vertebrae, the insertion by three main tendons, and the tripartite innervation. At the posterior end the three parts are most easily separated.

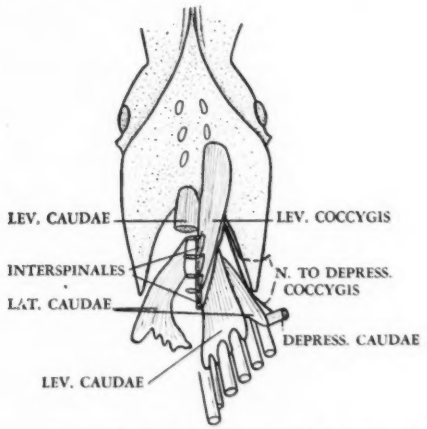


Fig. 15. *Coragyps atratus.* Dorsal view of the muscles of the tail. ×½.

Origin.—The origin is partly fleshy from a narrow line along the median dorsal surface of the ilium and from the transverse processes of the fused sacral vertebrae beginning with the third posterior to the acetabulum (fig. 15). It is fleshy from the lateral surface of the last two fused vertebrae. Anterior to the neural spine of the first caudal vertebra the medial edges of this pair of muscles lie side by side, but more anteriorly they are widely separated.

Insertion.—Tendinous on the anterolateral surfaces of the neural spines of the free caudal vertebrae and the pygostyle and partly fleshy on the dorsal surface of the first

free vertebra. The most superficial and largest tendon inserts on the anterolateral corners of the neural spines of caudal vertebrae 2, 3, 4 and 5; in one black vulture a part of this tendon inserted on the lateral surface of the pygostyle immediately anterior and ventral to the haemal canal. The intermediate tendon inserts on the dorsal surface of the base of the transverse processes of vertebrae 4 and 5, and the deepest tendon inserts in the same place on the third vertebra.

Innervation.—Dorsal branches of the caudal nerve emerge in front of the transverse processes of the first three free vertebrae. These three branches pass medial to the M. levator caudae and enter the different parts of the belly of M. levator coccygis on their medioventral edges.

Action.—If both muscles contract simultaneously, the tail is elevated and curved upward. If the muscle on one side only contracts, there is a weak lateral pull.

Comparison.—In all respects the M. levator coccygis is similar in *Coragyps*, *Sarcoramphus*, and *Cathartes;* it is better developed in *Sarcoramphus* (table 22B). In *Gymnogyps* the superficial tendon inserts on the neural spine of the fifth free caudal vertebra only, and the small, intermediate tendon inserts only on the dorsal surface of the transverse process of vertebra 5. There is no insertion on the pygostyle in this condor. The origin extends forward to the interacetabular region in *Vultur*, and the intermediate branch inserts tendinously on the ridge marking the lower margin of the articulation of the pygostyle. An additional large lateral fasciculus is developed in *Vultur* and is inseparable from the underlying M. levator caudae. Opposite the oil gland this fasciculus fans out to send tendinous branches to the dorsal surfaces of the bases of all the rectrices.

MM. INTERSPINALES

After removal of the skin on the dorsal surface of the tail these small muscles are visible between the neural processes of the free vertebrae (fig. 15). They are present in all the cathartids dissected but appear to be best developed in *Gymnogyps* and *Vultur* and least developed in *Coragyps*. In the chicken, du Toit (1913:179) found them "occasionally" as small muscle bands which are usually represented in the adult birds only by tendons. He regarded them simply as split-off parts of the M. levator coccygis.

The sole function is to aid the tail levators in flexing the tail upward. Their presence in adult cathartids is perhaps correlated with the minute and precise movements of the tail.

M. LEVATOR CAUDAE

Description.—Proximally this five-layered muscle lies just ventral to the M. levator coccygis. After emerging from beneath the M. levator coccygis the belly becomes thicker and wider (fig. 15).

Origin.—Tendinous and fleshy from the dorsal and anterior surfaces of the transverse processes of all free caudal vertebrae. The origin may extend on to the last sacral vertebra.

Insertion.—At the proximal end of the pygostyle the muscle forms a wide tendon which sends fingerlike tendons to the dorsomedial corners of the bases of rectrices 2, 3, 4 and 5. These tendons are in intimate contact with the fascia covering and connecting the bases of the rectrices. As can be seen in figure 15, a wider tendon goes to the anterolateral surface of the pygostyle and inserts on the thickened ridge immediately distal to the articulating surface. The bases of the five medial major upper tail coverts are buried in the inserting tendon.

Innervation.—By three branches of the caudal ? nerve which emerge dorsally behind the transverse processes of the first, second and third free vertebrae. The caudal nerve is that bundle of spinal nerves that passes caudally beneath the transverse processes of the free caudal vertebrae. Du Toit (1913: 181) found only one nerve twig entering the muscle, and that one came from the ventral side near the first caudal vertebra. He concluded that the muscle really belonged to the ventral musculature. In my specimens the nerves branched so near the vertebrae it was impossible to determine whether they were branches of the caudal nerve, as du Toit believed, or separate spinal nerves.

Action.—If both muscles act simultaneously the tail is elevated and the rectrices are adducted. Action on one side only produces a lateral pull on the pygostyle and rectrices. In either case the medial major upper coverts are retracted and elevated.

Comparison.—The muscle is identical in *Coragyps* and *Cathartes*. The origin in *Gymnogyps* is confined to the first four free caudal vertebrae and the last fused sacral vertebra. In addition, the part inserting on the pygostyle is a well developed tendon from the superficial slip of the muscle. This slip is separated from the rest of the belly for the distal two-thirds of its length. A small tendon inserts on the median side of the base of the lateral rectrix. The M. levator caudae in *Vultur* differs from that in *Coragyps* in only one way; the insertion on the pygostyle is in common with the insertion on the pygostyle of the lateral fasciculus of M. levator coccygis.

In *Sarcoramphus*, as in *Gymnogyps*, there is a tendon to the medial face of the base of rectrix 6. The tendons in the king vulture are incompletely separated; the insertion is more like a wide, thick tendon going to the dorsal surface of all rectrices.

The differences in *Gymnogyps*, along with larger size of the muscle, provide for stronger lateral movements of the pygostyle, and for more complete control of the rectrices because of an additional insertion on rectrix 6.

In table 22B note the weakness of this muscle in *Coragyps* as compared to the other cathartids.

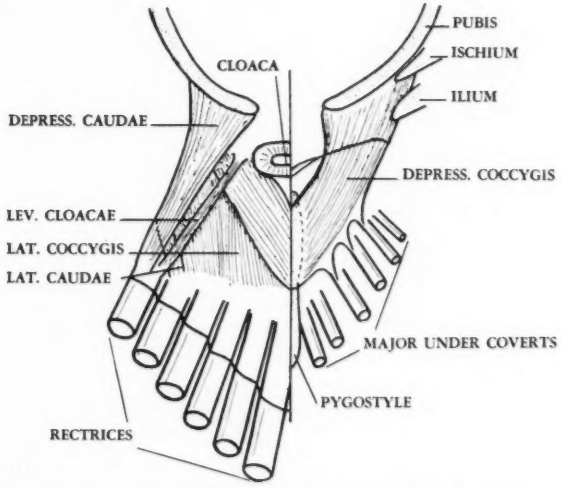


Fig. 16. *Coragyps atratus*. Ventral view of the muscles of the tail, ×1/2.

M. LATERALIS CAUDAE

Description.—The thickest and most fleshy part of the muscle lies laterally on the tail and extends to the base of rectrix 6. The medial part of the belly is short and gives rise to tendons to the bases of rectrices 3, 4 and 5 (fig. 15). Along the dorsal surface of the muscle lies a nerve which emerges through the belly of the muscle in the region of the second and third free vertebrae. It continues caudally to the skin and fascia overlying the bases of the rectrices.

Origin.—Tendinous from the tips of the transverse processes of the first three free vertebrae and from membranes between the ilium and the first two free vertebrae. At its most proximal point the origin is separated from the origin of M. levator caudae by

a large vein coming out anterior to the transverse process of the second vertebra. It is only at the origin that the three parts of the muscle may be observed, and even here the two most medial parts, from vertebrae 2 and 3, are essentially one.

Insertion.—Tendinous on the bases of rectrices 3 to 6 and to the fascia overlying them. The medial part of the muscle has a two-fold insertion; the dorsal part inserts widely on the medial surfaces of rectrices 3, 4 and 5, and the deeper part goes beneath the lateral part, inserting on rectrix 6, and traverses the lateral edge of the tail to insert on the *ventral* bases of rectrices 4, 5 and 6. The main insertion is by the large lateral part of the muscle on the upper and outer surfaces of rectrix 6, but this insertion is continuous medially with the insertion of the dorsal, medial part of the muscle (fig. 16).

Innervation.—By three spinal nerves which emerge posterior to the transverse processes of the first three free caudal vertebrae.

Action.—Slight upward flexion of the tail. However, the main function is abduction of the rectrices, for which the muscle is admirably adapted by its complex insertion which extends around the lateral edge of the tail.

Comparison.—The M. lateralis caudae shows much generic variation, but it is composed of two main parts in all the vultures dissected. The insertion of the lateral, superficial part on rectrix 6 is identical in all. In *Cathartes* this part arises from caudal vertebrae 2 and 3 and from the iliovertebral aponeurosis; in *Vultur* it originates from the tips of the transverse processes of the first three caudal vertebrae. In *Gymnogyps* the origin of the lateral part is the same as in *Coragyps*.

Still greater variation is exhibited by the medial part of the muscle. In *Cathartes*, *Gymnogyps*, and *Vultur* the superficial layer of this part is poorly developed in comparison to *Coragyps*. In *Cathartes* there is no direct insertion on any rectrix save rectrix 6, and the attachment is to the dorsal, lateral and ventral surfaces proximal to the insertion of M. depressor caudae. In *Gymnogyps* it arises from vertebrae 3 and 4 and is least developed; only fascial connections with the outer three retrices are present. The origin of this part in *Vultur* is limited to the tip of the transverse process of the third free vertebra. The deep slip of the medial part of the muscle in *Cathartes* originates partly from the tip of the transverse process of the second caudal vertebra, but its main origin is from fascia covering the proximal ends of the three lateral rectrices. It runs laterally to insert on the dorsal, lateral and ventral surfaces of rectrix 6 in common with the insertion of the lateral part of the muscle. In *Gymnogyps* the deep, medial slip arises from the transverse processes of free vertebrae 3 and 4 and from fascia over the dorsal surfaces of the lateral rectrices and inserts on the lateral surface of rectrix 6 and the ventral surfaces of rectrices 5 and 6. This same part in *Vultur* originates on the tip of the transverse process of the third vertebra and on fascia overlying the bases of rectrices 5 and 6.

In *Sarcoramphus* the M. lateralis caudae is similar to the same muscle in *Vultur*. However, the deep medial part is unusually large and goes as a fleshy muscle around to the ventral surface of the tail and inserts semi-fleshily on the ventral surfaces of the bases of rectrices 3 to 6 inclusive.

In the condition described for *Coragyps* contraction of any part of the muscle results in abduction of the rectrices and some upward flexion of the rectrices upon the caudal vertebrae. Such action is brought about in all the cathartids by contraction of the large, lateral slip of the muscle. In *Coragyps* action of the superficial, medial part affects rectrices 3, 4 and 5; in *Cathartes* rectrix 6; in *Vultur* rectrices 4 and 5 and in *Gymnogyps* rectrices 3, 4 and 5. The action is very weak in the latter. The deeper, medial fasciculus in *Coragyps* approximates rectrices 4, 5 and 6 and abducts them as a group. In *Cathartes* the deep slip abducts rectrix 6, but at the same time the origins on the dorsal surfaces of rectrices 4 and 5 may act as insertions. Thus, contraction of the part arising from the dorsal surfaces of the rectrices at a time when rectrix 6 is abducted would also abduct rectrices 4 and 5. The same situation exists in *Gymnogyps*, *Sarcoramphus* and *Vultur*. Regulation of the relative position of rectrix 5 and rectrix 6 is another possible function as is rotation (upward or downward) of the lateral rectrices. In other words, the muscle may aid in elevating or depressing the lateral edge of the tail by moving the bases of rectrices 5 and 6 up or down.

Sarcoramphus has by far the largest muscle. In table 22B note the small size of the muscle in *Cathartes* and *Gymnogyps*. Small size in addition to more lateral insertions probably are adaptations to delicate movements of the lateral rectrices during soaring.

M. DEPRESSOR CAUDAE

Origin.—The M. depressor caudae originates by fleshy fibers from the tip of the ischium and the medial face of the pubis immediately above the origin of M. flexor cruris medialis. The origin from the ischium is usually small. Caudally the origin may extend on to the cloacal fascia and may even fuse with the median part of the origin of the M. depressor coccygis (figs. 15 and 16).

Insertion.—The insertion is fleshy on the ventral base of rectrix 6, in common with the insertion of the lateral part of the M. lateralis caudae.

Innervation.—A double innervation occurs here. A branch of the obturator nerve passes posteriorly between the heads of the two adductor muscles and beneath the middle of the M. caudofemoralis to enter the lateral face of the M. depressor caudae near its origin. From inside the ilium a branch of the N. pudendus passes beneath the tendon of M. caudofemoralis, parallels the lateral surface of the M. lateralis caudae, and enters the M. depressor caudae near its insertion on rectrix 6.

Action.—When contracting in unison the muscles depress the tail, especially the lateral rectrices. At the same time the rectrices would tend to spread out fanlike. Unilateral action by one muscle tilts the tail, a movement often observed in soaring birds.

Comparison.—Table 22B demonstrates that this muscle is best developed in *Cathartes* and is poorly developed in *Coragyps*. In *Vultur* and *Gymnogyps* it is of about equal relative bulk and is only slightly weaker than in *Cathartes;* in *Sarcoramphus* the muscle is intermediate in bulk between *Coragyps* and the condors.

In the turkey vulture and the South American condor the insertion is wider and extends medially on to the base of the fifth rectrix. In the turkey vulture and in the California condor the origin expands medially to the midline on the fascia ventral to the cloaca. In *Gymnogyps* a small tendon beneath the cloaca may connect the muscles of the two sides. Two-thirds of the origin in *Vultur* is from the ischium; about one-half of the origin is ischial in *Gymnogyps*. Extension or movement of the origin on to the ischium as in these two condors is significant because the direction of the fibers is more favorable for abduction of the rectrices. Medial extension of the origin beneath the cloaca increases the effective power for depression of the tail.

Therefore, considering relative volumes, origins and insertions of the muscle, one must conclude that for depression of the tail the muscle is most effective in *Cathartes*, *Gymnogyps*, and *Sarcoramphus*, least effective in *Coragyps* and intermediate in *Vultur*. For abduction of the rectrices the muscle is most efficient in *Vultur* and *Gymnogyps* and much less effective in *Cathartes*, *Sarcoramphus* and *Coragyps*.

M. LEVATOR CLOACAE

Description.—The M. levator cloacae (M. suspensor ani of du Toit, 1913:186-187) lies beneath the medial edge of M. depressor caudae and is parallel to it. In *Coragyps*, *Gymnogyps*, *Sarcoramphus* and *Vultur* these two muscles are entirely separated, but the M. levator cloacae of *Cathartes* is inseparable distally from the M. depressor caudae. M. levator cloacae probably arose from the M. depressor caudae as is indicated by its origin, insertion and innervation. Since the origin of this latter muscle may extend on to the cloacal fascia, it would be a simple matter for the medial edge to split off and move a short distance dorsocaudally to form the M. levator cloacae (fig. 16).

Origin.—Fleshy on the fascia lateral to the cloaca.

Insertion.—Fleshy on the ventral surface of the base of rectrix 6 immediately medial and proximal to the insertion of M. depressor caudae. This attachment is the functional origin.

Innervation.—By the same branch of the N. pudendus that serves the proximal end of the M. depressor caudae. This indicates the probable origin of the muscle.

Action.—Elevation of the tail automatically raises the cloacal orifice. The muscle thus enables the bird to discharge fecal material with minimum soiling of the feathers. In copulation the muscle probably aids in effecting juxtaposition of the cloacae by moving the opening upward and to either side. This muscle is the only one in position to perform such a function.

Comparison.—The M. levator cloacae in *Cathartes* is very small and is inseparable distally from the M. depressor caudae, which entirely covers it ventrally. In *Vultur* and *Gymnogyps* the distal attachment is to the bases of major lower coverts 5 and 6. The proximal attachment is the same in all the genera. However, the muscle is almost entirely tendinous in *Sarcoramphus* and *Vultur*.

M. DEPRESSOR COCCYGIS

Description.—Dorsal to the origins of Mm. depressor caudae and levator cloacae is the M. depressor coccygis, a powerful muscle that meets its counterpart in the midline beneath the anterior half of the ventral edge of the pygostyle (fig. 16). Lateral to the cloaca the muscle is divided transversely by a tendon. The tendon extends medially and meets the tendon of the opposite side immediately dorsal to the cloaca; it is in intimate contact with the fascia above the cloaca.

Origin.—Fleshy from a line running from the inner face of the ischium at its fusion with the ilium posterolaterally to the tip of the free end of the pubis. The origin is medial to that of the M. depressor caudae. Posteriorly the origin is very thin and may extend medially on to the ventrolateral cloacal fascia.

Insertion.—Fingerlike tendons are attached to the median sides of major under coverts 3, 4 and 5. Although the muscle is in close contact with the fascia above coverts 1 and 2, no definite tendons are formed for an insertion on them. The main insertion is by fleshy fibers on the ventrolateral corner of the anterior half of the pygostyle.

Innervation.—Two nerve twigs enter this muscle. The same branch of the N. pudendus internus that serves the Mm. depressor caudae and levator cloacae sends a twig to the M. depressor coccygis near the origin of this muscle. Another nerve (N. pudendus externus) parallels the lateral edge of the muscle and enters the external face of the middle of the belly. A double innervation of this muscle is significant in view of the complete separation of the muscle by the transverse tendon.

Action.—Undoubtedly the main function is depression of the entire tail, but simultaneously the muscle adducts the major under coverts and depresses the cloaca. The strong tendon connecting the two muscles of this pair precludes strong action by one muscle alone, and therefore largely eliminates the possibility of lateral movements that this muscle might otherwise effect. At the same time it is a strengthening device for better depression of the tail. It is this muscle along with the M. lateralis coccygis that forms the chief mechanism for holding the tail in the proper vertical position during flight. Since the tail in soaring birds provides a good part of the supporting surface it is vital that strong muscles hold it down flat to prevent the loss of supporting air beneath. Thus this muscle may not actively depress the tail at all times; it may brace against the upward force of air beneath the tail. Development of this muscle is not, therefore, correlated solely with ability to depress the tail actively. It is more intimately related to the weight of the bird, the length of rectrices and the ability to soar. This may explain the large size of the muscle in *Gymnogyps* which does not use the depressed tail for a braking device.

Comparison.—In *Cathartes*, *Sarcoramphus* and *Vultur* the fleshy parts of the muscles do not meet in the midline; there is only strong fascial attachment to the pygostyle. In *Vultur* the tendon dividing the muscle into two parts is strongly connected to the ventral surface of the M. lateralis coccygis which lies dorsal to the M. depressor coccygis. In *Sarcoramphus* the chief insertion is on coverts 2, 3 and 4, rather than on 3, 4 and 5 as in *Coragyps*. In *Gymnogyps* the two inner lesser under coverts are imbedded in the flesh of the muscle which inserts fleshily on the pygostyle and tendinously on major under coverts 1 to 4 inclusive. Thus the differences between the cathartids are of little func-

tional importance; even the tendinous attachment to the M. lateralis coccygis in *Vultur* is unimportant since the function of the muscles is unchanged by this arrangement.

Table 22B indicates that the muscle is relatively strongest in *Sarcoramphus* and *Vultur* and weakest in *Coragyps*. It is slightly weaker in *Gymnogyps* than in *Cathartes*.

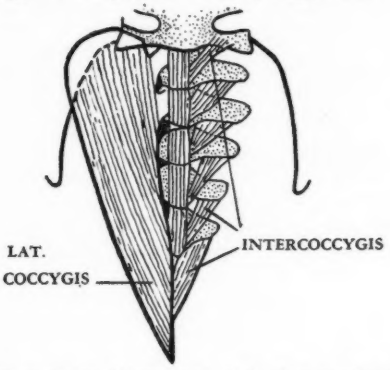


Fig. 17. *Coragyps atratus*. Ventral view of the deep muscles of the tail, ×1.

M. LATERALIS COCCYGIS

Description.—After removal of the Mm. depressor caudae, levator cloacae and the depressor coccygis this muscle may be observed to cover the entire ventral surface of the tail except in the mid-region beneath caudal vertebrae 1 and 2 (fig. 16). Laterally it is bounded by the M. lateralis caudae; the two are in intimate contact. The muscles of the opposite sides meet in the midline beneath the anterior part of the pygostyle and the three vertebrae anterior to it. This junction is entirely encased by strong, white fascia in which is imbedded the tendon of the M. caudofemoralis. Along the vertebral column the dorsal surface of the muscle may be separated into many fasciculi. Shufeldt (1890: 315-317) terms some of these fasciculi the M. infracoccygis. The fasciculi between successive transverse processes of the vertebrae are called the Mm. intertransversarii by du Toit (1913:180) who fails to mention other muscle slips between successive haemal arches of the vertebrae. I consider all these slips as parts of the M. lateralis coccygis. The parts between the haemal arches are the ventral counterparts of the Mm. interspinales between the neural arches.

Origin.—Fleshy from the posteroventral surface of the ilium near the midline and tendinous from the underside of the ends of the transverse processes of the first three free caudal vertebrae. Various small fasciculi arise by fleshy fibers from the posterior edges of the transverse processes and from the haemal arches.

Insertion. The main insertion is partly fleshy on the ventrolateral corners of the anterior two-thirds of the pygostyle immediately dorsal to the insertion of M. depressor coccygis. There is also strong fascial attachment to the bases of rectrices 1 to 4. Some slips insert on the anterior faces of the haemal arches, and others from the transverse processes insert on the lateral surfaces of the centra.

Innervation.—All parts of the muscle are innervated by ventral branches of the caudal nerve.

Action.—Simultaneous action by the muscles causes strong depression of the tail. Weak downward flexion of the tail might result from contraction of the fasciculi between the haemal arches. Contraction of the muscle on one side only abducts the tail. A similar abduction, but very weak, is occasioned by the slips between the transverse processes and the centra of the following vertebrae (see fig. 16 and the discussion of the function of M. depressor coccygis.)

Comparison.—Similarly arranged in all the vultures. In *Gymnogyps* the *ilial* origin is weakest; the main origin is from the under surfaces of the first four or five caudal vertebrae. In *Vultur* there is strong fascial insertion on the bases of all the major under tail coverts.

This muscle is remarkably powerful in *Coragyps*. It is next strongest in *Cathartes*, somewhat weaker in *Gymnogyps* and *Vultur*, and is smallest in *Sarcoramphus*, but even here it constitutes 25 per cent of the tail musculature. The relatively large size of the muscle in *Coragyps* is significant; it provides greater power for lateral movements through a wide arc.

Discussion of the Tail Musculature

Although the function of each muscle has already been discussed briefly, no clear understanding of the action and the interaction of muscles can be had without considering them as members of functional groups. A comparison of the use of the tail in the various cathartid genera has been given previously (p. 623). Still another major factor necessary to an understanding of the function of the muscles of the tail is the relative length of the rectrices. *Coragyps* has a short square tail averaging (in 8 specimens) 7 inches in length. Thirteen turkey vultures showed an average tail length of 9.9 inches; 7 *Gymnogyps* averaged 13.6 inches: 3 specimens of *Vultur* yielded an average tail length of 14.3 inches, and 2 *Sarcoramphus* 8.5 inches.

The total volume of muscles (except M. caudofemoralis) operating the tail is an index to the power of its movements, but due to differences in weights of the various genera it is difficult to use. However, these volumes may be used in conjunction with average weights of the genera to obtain a rough, yet significant ratio. Using the volumes of tail muscles as determined in one specimen of each genus, we find that the ratio of tail muscle volume to body weight is 2.14 in *Cathartes*, 1.60 in *Coragyps*, 1.13 in *Sarcoramphus* and 0.46 in *Gymnogyps*. The last ratio is meaningless because the specimen dissected was emaciated. If the weight of the specimen dissected is used, the more accurate ratio of 0.98 is obtained.

The ratios indicate that the tail muscles of *Gymnogyps* are not as large and powerful as they are in the other three genera. When the tail length is considered, it may be observed that the musculature for the tail is as well developed in *Coragyps* as in *Cathartes;* perhaps it is somewhat better developed. *Sarcoramphus* is intermediate to the California condor and the small vultures.

Tail levators.—In this category fall the Mm. levator coccygis, levator caudae and lateralis caudae. Only the superficial, medial slip of the latter muscle should be included here. As may be observed in table 22B, the levators constitute the greatest per cent of the volume of the tail musculature in *Sarcoramphus* and *Gymnogyps*, and the smallest per cent in *Coragyps*. However, the larger, superficial, medial layer of the M. lateralis caudae in *Coragyps*, *Sarcoramphus* and *Vultur* aids the true levators. Thus elevation of the tail is stronger in *Vultur* than in *Cathartes*. Since the tail feathers of *Coragyps* are so much shorter than those of *Cathartes* and the levator musculature is about equally developed, we must conclude that the tail may be raised more easily in the former. The series from powerful to less powerful levation is *Sarcoramphus*, *Gymnogyps*, *Vultur*, *Coragyps* and *Cathartes*.

Tail depressors.—Included here are the Mm. depressor caudae, depressor coccygis, lateralis coccygis and levator cloacae. Table 22B indicates that the depressors are best developed in *Coragyps* and *Cathartes* and weakest in *Sarcoramphus*. In all cathartids the ventral, depressor musculature is significantly stronger than the levator musculature.

Although listed functionally as a depressor, the M. depressor caudae is important also in tail-tilting. In addition it aids in spreading the rectrices as does the M. lateralis caudae. The muscles causing lateral movement of the tail include both depressors and levators. Thus such gross ratios for groups of muscles as I have used are subject to considerable error due to the varied functions of individual muscles.

TABLE 22 A.—Volumes of Individual Tail Muscles in Cubic Centimeters.

	Cathartes	Coragyps	Gymnogyps	Vultur	Sarcoramphus
Depressor caudae	1.50	0.40	1.50	4.20	0.80
Levator cloacae		0.15	0.20	0.20	0.10
Depressor coccygis	1.50	0.60	1.60	6.90	2.00
Lateralis coccygis	3.40	4.10	3.50	10.50	2.35
Levator coccygis	0.85	0.70	1.70	8.20	1.15
Levator caudae	1.30	0.40	2.00		1.30
Lateralis caudae	0.60	0.80	1.10	3.70	1.65
Total Volume	9.20	7.20	11.60	33.70	9.35

The general impression gained from the foregoing analysis is that the tail musculature in *Coragyps* is more weakly developed than in other cathartids, partly perhaps to conform with the shorter rectrices. However, the tail musculature is not reduced as much as are the rectrices. The Mm. interspinales and Mm. adductor rectricum are weakest in *Coragyps* and strongest in *Gymnogyps* and *Vultur;* the M. depressor caudae is also poorly developed in *Coragyps*. The lateralis coccygis is the only muscle that is relatively stronger in *Coragyps* than in the other genera. The strong depressors of the tail, Mm. depressor coccygis and lateralis coccygis are more proximally and medially inserted in *Coragyps*. Thus they are more capable of sudden gross movements than are the more distally and laterally inserted muscles in *Gymnogyps* and *Vultur*.

The muscles (Mm. adductor rectricum, levator caudae, lateralis caudae and depressor caudae) which are intimately connected to the rectrices are best adapted to control the rectrices in *Gymnogyps*, *Sarcoramphus* and *Vultur*. The Mm. adductor rectricum and M. depressor caudae are larger in these forms; the levator caudae in *Sarcoramphus* and in *Gymnogyps* has an additional insertion on rectrix 6, and the latter has a separate insertion on the pygostyle. The Mm. levator coccygis and levator caudae insert farther distally in *Gymnogyps* and *Vultur;* the M. depressor caudae originates farther laterally in these genera and thus provides a better mechanism for abduction of the rectrices. In *Gymnogyps* the origin of M. lateralis coccygis is more distal; this decreases its ability to depress the tail as a whole.

We may see from the above discussion that the muscles of *Gymnogyps* and *Vultur*, and to some extent of *Sarcoramphus*, are so placed as to give

more delicate control of the rectrices and the tail as a unit. That is, certain of the muscles insert farther laterally and distally in order to effect precise movements. However, these movements are as a rule more slowly executed. *Cathartes*, in this respect is intermediate, and yet is much nearer the condors than is *Coragyps*.

TABLE 22 B.—Ratios of Individual Muscle Volumes to Total Volume of Tail Musculature.

	Cathartes	Coragyps	Gymnogyps	Vultur	Sarcoramphus
Depressor caudae	16.30	5.60	12.9	12.10	8.56
Levator cloacae		2.10	1.70	0.60	0.86
Depressor coccygis	16.30	8.30	13.80	20.50	21.40
Lateralis coccygis	37.00	57.00	30.10	31.00	25.00
Levator coccygis	9.20	9.70	14.70	24.30	12.30
Levator caudae	14.10	5.60	17.20		13.90
Lateralis caudae	6.50	11.10	9.50	11.00	17.65
Total Per Cent	99.4	99.4	99.9	99.5	99.67

Table 23.—Synonymy of the Tail Muscles.

Shufeldt, 1890	du Toit, 1913	Fisher
levator coccygis	levator coccygis (part)	levator coccygis
levator caudae	ilio-coccygeus (part)	levator caudae
depressor caudae	pubi-coccygeus externus	depressor caudae
depressor coccygis	depressor coccygis	depressor coccygis
lateralis caudae	ilio-coccygeus (part)	lateralis caudae
lateralis coccygis	pubi-coccygeus internus	lateralis coccygis
infracoccygis	.....	infracoccygis
.....	adductor rectricum	adductor rectricum
.....	suspensor ani	levator cloacae
.....	levator coccygis (part)	interspinales

Use of the Hind Limb

A discussion of the major uses of the hind limb may be divided into four parts, the function in movement on the ground, in feeding, in the takeoff from the ground or the perch, and in perching itself. A brief description of the action of the leg in the California condor will be given, with which the action in other vultures will be compared.

On level ground the unfrightened condor usually walks slowly, with the head up and the body fairly erect. At the least sign of haste the gait becomes an awkward, shuffling gallop or a shambling hop. In greater haste they may break into a definite gallop, flapping the wings to accelerate the speed. Bent (1937: 8) quotes Townsend in saying in regard to the condor, "in walking they resemble a Turkey, strutting over the ground with great dignity; but this dignity is occasionally lost sight of, especially when two are striving to reach a dead fish, which has just been cast on the shore; the stately walk then degenerates into a clumsy sort of hopping canter, which is anything but graceful."

The legs in birds which are galloping exhibit movements similar to the movements of the hind legs of a galloping horse. Usage of the term "gallop"

is often restricted to quadrupedal animals, but because of the similarity to movements of the legs of the vultures the term is employed in this study. Any small obstruction such as small rocks, tall grass or twigs hampers them considerably. If they are galloping, they may be thrown off balance easily. In such cases the wings are extended to regain the posture.

When running for a takeoff, they may use a shuffling gallop or they may run. Hopping may occur briefly at the outset of the run for the takeoff. Runs for the takeoff average twenty-five to forty feet in length. However, if there is any prominent object such as a boulder, they frequently hop on this before starting to fly; the wings usually are flapped to aid in raising the bird to the prominence. In taking off from a perch the springing action of the legs is slight. As suggested previously, the bird crouches deliberately prior to flapping its wings. Apparently the feet are lifted from the perch by the action of the wings. If it is at all possible the bird simply steps over the edge of the limb of the tree or the cliff on which it has been resting.

For perches, condors seem to need wide flat surfaces. Rocky potholes in cliffs, large rocks and large branches in dead trees are most frequently used; in trees the minimum diameter of the branch used is about three or four inches. Of course part of the need for large branches results from a need for strong support for the heavy body, but the weak foot equipped with short claws and lacking well developed tarsal muscles is a major factor. If condors remain on a perch for some time, they invariably ease the strain on the legs by resting the breast on the perch to support the weight of the body. After they settle down for the night and before they start to move in the morning they may be observed in this position. Another function of crouching on the perch is to lessen wind resistance and to aid in maintenance of their position on the perch. Watson (1869) believed crouching aided in holding the toes flexed about the perch.

When sunning or preening, the California condor often stands on one foot, but it never does so for long. The foot may be moved forward to the shoulder region to scratch the head or it may be fully extended posteriorly below the level of the perch. On the perch the California condor is seldom as erect as are *Coragyps, Cathartes* and *Sarcoramphus*.

The leg takes less part in feeding in *Gymnogyps* than in the other vultures. The legs are used indirectly in pulling off parts of carcasses; the bill is hooked into the flesh and the bird backs away. All dragging or movement of food is accomplished in this way. Seldom does a condor stand on small bits of flesh and tear at it with the bill in the manner of strong-taloned hawks. When a condor does stand on its food to tear off bits of it, the weight of the bird and nothing else holds the meat in place. Most food is snipped from the carcass by a rapid, continuous scissor-like action of the mandibles.

The black vulture is more agile on the ground than the California condor. Saunders (1906:166) describes their movements as follows: "When the vulture is taking his time about getting around, he moves with a very solemn, sedate walk, carefully placing one foot in front of the other. When he is in a hurry,

however, he slightly spreads his wings and indulges in what looks like hopping but is really a very one-sided run. At first sight he seems to put both feet on the ground at once, but in reality he puts the left foot first and takes his long step with the right foot." McIlhenny (MS) describes the locomotion on level terrain. When walking, *Coragyps* takes short steps with head up and tail raised above the tips of the wing; when greater speed is necessary, they gallop. That is, they progress with one foot ahead of the other. Although the black vulture walks and runs with greater ease than does *Gymnogyps*, it is not so graceful as the chicken. Evans (1899:140) describes the gait of *Coragyps* as shuffling. Small obstructions in the path of movement bother them very little; they either turn sharply to one side at full speed (something the condor does not do) or merely spring over the rock, twig or tuft of tall grass.

The takeoff run is shorter in *Coragyps;* if a strong wind is blowing, the bird faces it and hops two or three times with wings extended and then springs into the air. In the absence of strong wind they jump three to seven times with wings extended and then spring into the air. Audubon (1834:50) noted that "before rising from the ground, they are obliged to take several leaps, which they do in an awkward sidelong manner." If the ground slopes, they turn to face downhill, crouch, spring up and start flapping immediately. When leaving a perch, the black vulture either jumps over the edge or springs up and forward, flapping the wings at the same time.

Coragyps occasionally perches temporarily on telephone wires or the top strand of a barbed wire fence; frequently they alight in the leafy twigs on the tops of trees or the tips of limbs. However, they are more often seen on bare limbs, one or two inches in diameter, on the ridgepoles of buildings and on fence posts. Seldom do they rest the breast on the perch; even when roosting they may stand hunched over on the legs.

In the active predation which the black vulture often undertakes the legs function importantly. McIlhenny (MS and 1939) found groups of black vultures, never a single individual, killing small animals such as opossums, skunks, and newly born pigs, calves and colts. The vultures surround the animal, hook their sharp bills into the skin in various places and pull backward strongly. The prey is literally torn apart. If the carcass needs further division the vulture usually hops up on it and holds it with the weight of the body; the bill is hooked into the flesh almost between the feet. Then with strong rapid jerks, in which the muscles of the neck, back and legs participate, a chunk is torn off. Occasionally the wings are flapped to give added backward force. An excerpt from a letter from McIlhenny will illustrate the great power and leverage of this tearing action. He states, "frequently, when banding vultures, my men who use heavy gloves, and have their arms wrapped in burlap when handling the vultures, catch the vultures by the neck, and frequently lose them by the vultures placing its two feet against the man's hand or arm, and pulling back with such strength that its head and neck are pulled from the man's grasp. This is not an unusual occurrence."

Bent (1937:36) also noted the force used in pulling food apart. He stated "in tearing off choice morsels from the carcass with their bills the vultures

brace their feet firmly on the ground and flap violently with their wings to aid them in pulling away."

On the ground *Cathartes* is not as awkward as *Gymnogyps*, but neither is it as agile as *Coragyps*. Its locomotion is similar to that of the California condor, but perhaps as a result of its lighter weight it moves more easily, without stumbling over small obstructions. The run for the takeoff is of shorter length than in *Gymnogyps*. *Cathartes* stands more erect on the ground and on the perch.

The culminating action of the takeoff run in the turkey vulture is not as definite a spring as it is in the black vulture, and in leaving a perch *Cathartes* resembles *Gymnogyps*.

The turkey vulture uses perches similar to those necessary for the California condor, but in addition it perches on smaller branches. Seldom, if ever, does it alight on objects with a diameter as small as that of a telephone wire or wire fence.

Cathartes is intermediate between *Gymnogyps* and *Coragyps* as regards the function of the hind limb in feeding.

No information on *Vultur* and *Sarcoramphus* has been available, but photographs indicate that the body stance is similar to that in *Coragyps* and is more erect than in *Cathartes* and *Gymnogyps*.

Position of the legs beneath the body is variable. In *Cathartes* and *Gymnogyps* there is a tendency toward a graviportal stance; that is, a vertical line through the acetabulum to the ground would pass through the femur, tibia and tarsus. In *Coragyps* the distal segments (tibia, tarsus and foot) are more medially located beneath the body. Photographs of *Vultur* and *Sarcoramphus* indicate a similar condition. Movement of the femur is restricted in all New World vultures.

No cathartid vulture is capable of carrying anything in its feet! The intramembral proportions of the foot, its weak musculature and the absence of talons preclude grasping action, yet Housse (1940) credits *Vultur* with carrying objects, and Jones (1935) reports one case in which *Cathartes* carried a snake in its feet!

Bones of the Pelvic Girdle and the Hind Limb

SYNSACRUM

The shape of the synsacrum is a good indicator of the build of the entire body. For example, the ratio of interacetabular width to synsacrum length (midline length) in *Cathartes* reflects the heavy, broad body structure. It is significant that this ratio is high in both *Cathartes* and *Sarcoramphus* since, as will be shown later, the bones of the hind limb indicate that these two are the least cursorially adapted of the vultures. Greater width in these vultures is also indicated by the greater breadth between the posterior iliac crests at their widest point (iliac width to synsacrum length ratios in table 25); however, anteriorly the synsacrum is narrow in *Sarcoramphus*. The ischium extends farther posteriorly in *Sarcoramphus* and *Coragyps* than in the others. This is important since many of the postfemoral muscles arise from the distal parts of the ischium. Greater posterior extent of this bone permits more posterior origin of the muscles, which in turn increases their vector of effective pull by directing their force more nearly at right angles to the femur. Thus a more effective force may be exerted upon the femur in walking, or upon the synsacrum if the muscles contract when the leg is motionless and firmly planted

upon the ground. The pull upon the postfemoral part of the synsacrum is an aid to the maintenance of an upright body position. All other factors being equal, in *Coragyps* and *Sarcoramphus* there is a possibility of more powerful muscular action. This may in part account for the fact that *Coragyps*, at least, holds the body more erect than do *Cathartes* and *Gymnogyps*. Unfortunately information as to the body position in *Sarcoramphus* and *Vultur* is not available.

TABLE 24.—Average Trunk Length in Millimeters*.

	Length from last cervical to last free lumbar vertebra		Preacetabular length of pelvis		Total trunk length
Gallus	65.0	(2)	42.8	(2)	107.8
Pandion	76.7	(4)	35.9	(5)	112.6
Aquila	108.0	(5)	68.8	(6)	176.8
Cathartes	72.4	(7)	51.9	(8)	124.3
Coragyps	85.0	(4)	55.0	(4)	140.0
Gymnogyps	113.5	(2)	103.5	(2)	217.0
Sarcoramphus	94.3	(2)	65.3	(2)	159.6
Vultur	148.5	(2)	105.9	(2)	254.4

* Numbers in parentheses indicate numbers of specimens measured.

The ratios of ischial length to synsacral length in *Astur* and *Aquila* support the foregoing theory of the adaptive value of a relatively long ischium. In these birds and in the cathartids the value is apparent when one sees them pulling on carcasses; the feet are firmly braced, and the bill is hooked into the carcass from which pieces are pulled by quick jerks of the entire body. It is evident that postfemoral muscles are important in this feeding habit.

Still another modification increases the effectiveness of the postfemoral leg muscles. On plates 9 and 10 it may be observed that in *Aquila*, *Buteo*, *Astur* and *Accipiter* the postacetabular portion of the synsacrum is curved ventrally and anteriorly. This increases the effective power of the muscles originating from the ischium by bringing the longitudinal axis of the muscles more nearly parallel to the axis of desired action.

TABLE 25.—Ratios of Parts of Synsacrum.

	Accipiter	Astur	Aquila	Buteo	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Interacetabular width: length	43.2	47.3	42.8	44.6	50.4	40.2	37.8	48.3	38.5
Anterior width: length	47.1	51.0	52.2	55.4	53.6	45.3	46.1	44.7	41.6
Iliac width: length	67.1	73.0	65.6	70.2	67.9	58.7	57.4	63.2	53.2
Ilium, postacetabular length: length	48.3	52.5	52.6	54.6	47.4	52.6	48.5	58.2	47.3

In the synsacrum of three *Gymnogyps* and two *Vultur* skeletons there were 15 fused vertebrae. One skeleton of *Sarcoramphus* showed 15 and the other 14 sacral vertebrae. In one-half of the synsacra of *Cathartes* there were 14 such vertebrae; in the other half 15 could be counted. It was the addition of one caudal vertebra that caused the increased number in each instance. The same was true in *Coragyps*, one-half showed 14 and one-half 15 due to the presence of one more caudal vertebra. Judging from the long series of accipitrid skeletons available, the usual number is 13. This was consistently true in the accipitrines, but in the buteonines there frequently was an added caudal vertebra. In one example of *Aquila* a thoracic vertebra was fused in. No doubt

age plays some part in the fusing of the sacral vertebra, but in individuals of known age I found no large differences in fusion of caudal vertebrae correlated with age. It was an immature specimen of *Sarcoramphus* that had an extra vertebra; in *Gymnogyps* no variation was seen in the extent of fusion, although one skeleton was of a juvenal bird. It is impossible to ascertain whether the variation within the family is phylogenetic or adaptational. However, there was more specific variation in the cathartids and a greater number of vertebrae involved. The increase in number in the Cathartidae always occurred by the addition of a caudal vertebra; this is shown by the corresponding decrease in caudal numbers as well as by direct study of the synsacrum. I think it is possible that the number of fused vertebrae in the sacral region has increased in the vultures as a means of strengthening this area for better horizontal support of the body and the tail, with less exertion on the part of the muscles. However, in the Accipitridae the posterior part of the synsacrum turns more abruptly ventrally posterior to the acetabulum. It may be that this turning of the ilium combined with lesser bending in the sacral vertebrae has resulted in the freeing of a vertebra. But in this case one would expect the number of vertebrae to be as variable in the accipitrids as in the cathartids, and it is not.

Closure of the dorsal spaces between the transverse processes of the sacral vertebrae is variable. In *Cathartes* the most fenestrated condition exists (plate 9). *Coragyps* shows more openings along the column than the remaining cathartids. The immature skeleton of *Sarcoramphus* is more fenestrated than that of the adult. This leads to the conclusion that some, but not all, of the interstices are due to immaturity. Accipitrids show perforations along the vertebral column only in the region of the last two or three vertebrae; *Gymnogyps* and *Vultur* also exhibit openings only in this area. Shufeldt (1909:44) made the same observations on the closure of the foramina between the transverse processes.

TABLE 26.—Average Measurements of Synsacrum.

	Length anterior to acetabulum	Length in midline	Width through acetabulum	Width anterior	Width between iliac crests	Length of ilium posterior to acetabulum
Accipiter	31.5 (6)	43.5 (6)	18.9 (6)	20.5 (5)	29.2 (6)	21.0 (6)
Astur	39.0 (2)	52.6 (2)	24.9 (2)	26.8 (2)	38.4 (2)	27.6 (2)
Aquila	67.3 (6)	90.6 (6)	38.8 (7)	47.3 (7)	59.4 (6)	47.7 (7)
Buteo	41.9 (4)	56.0 (4)	25.0 (4)	31.0 (4)	39.3 (4)	30.6 (4)
Cathartes	52.5 (8)	79.8 (8)	40.3 (8)	42.9 (8)	54.3 (8)	37.9 (8)
Coragyps	55.0 (4)	83.0 (4)	33.4 (4)	37.6 (4)	48.7 (4)	43.7 (4)
Gymnogyps	103.5 (3)	137.0 (3)	51.8 (3)	63.1 (3)	78.6 (3)	66.5 (3)
Sarcoramphus	65.3 (2)	94.8 (2)	45.8 (2)	42.4 (2)	59.9 (2)	55.2 (2)
Vultur	108.5 (2)	151.5 (2)	58.5 (2)	63.2 (2)	80.8 (2)	71.9 (2)

It may be observed in plate 10 that cathartids possess more depth at the anterior end of the synsacrum in the region of the fused lumbar vertebrae than do the Accipitridae. The height of the vertebrae in the Cathartidae diminishes rapidly posteriorly. The decrease in the height is much more gradual in the hawks and eagles. Depth in the acetabular area is considerably greater in the accipitrids, due in part at least to the angle the postacetabular region forms with the preacetabular synsacrum.

The ilium extends forward in the Accipitridae to cover the first sacral vertebra; in *Coragyps* the ilium overlies most of this vertebra, but in the other cathartids the entire first vertebra and often part of the second is exposed. The crests of the ilia lie in contact anteriorly in *Aquila*, *Astur* and *Accipiter* and in most cathartids. In *Cathartes*, however, they are separated by a relatively broad area of the vertebral column; *Buteo* exhibits some space between the ilia. As a rule the medial dorsal crests of the ilium in the Cathartidae are not raised as high above the level of the intervening vertebral column as they are in accipitrids. Especially is this true in the acetabular region. A raised crest provides a stronger point of origin for the iliotibialis and iliofibularis muscles. The anterior half

of the face of the ilium is nearly horizontal in *Cathartes;* other vultures show a horizontal plane only in the anterolateral corner of the ilium. *Aquila* and *Buteo* reflect the steeper inclination of the ilial face that is to be found in the accipitrines. Viewed from the top (or the side) (plate 10), the posterior dorsal iliac crest in accipitrids shows a sharp curvature ventrally and medially toward its fusion with the ischium.

The ischium faces upward and outward. Thus a deep, elongate fossa is formed for the large muscles present here—the adductors, the obturators, the crural flexors and the ischio-femoralis. The lateral shelf-like extension of the iliac crest over the anterior part of the ischium and its ventral deflection provide better opportunity for muscular action in two ways—by providing a larger area for the fleshy origin of the muscles named and by moving this area of origin to a position in which the muscle fibers more nearly parallel the most efficient vector of force. In cathartids the iliac crest does not curve ventrally so sharply; the medial curvature is slight and the ischium faces laterally for the most part. Therefore, the fossa for muscle origin is relatively wider but is much shallower and shorter (plates 9 and 10). In addition there is a "v-shaped" notch between the ends of the ilium and the ischium in vultures; no opening is present there in hawks. Presence of this notch is a distinguishing feature of the cathartid pelvis. Shufeldt (1909: 46) stated that "this notch is acute or angular in the condors and the King Vulture, but rounded in the Turkey buzzard and the Carrion crow. . . ." A glance at plate 10 will verify the correctness of this observation. Since the anterior part of the ilium is expanded and lies in a more horizontal position in the vultures, the transverse processes do not extend as far laterally on it and thus the lateral edge of the ilium is not as well supported as in the hawks. This weakness is most evident in *Cathartes.*

Between the antitrochanter and the dorsal iliac crest there is frequently a relatively deep pit, sometimes with pneumatic foramina, in *Aquila* and *Buteo. Coragyps* possesses only the foramina here, and no indications of either pit or foramina are present in the other genera.

Development of the pubis is weak in the Accipitridae; in *Astur, Accipiter* and *Buteo* it is an extremely fragile bone extending caudally only as far as the posterior end of the obturator foramen where it fuses to the ischium, thus forming the lower edge of the foramen. Frequently another vestige of the bone may be found extending back from the lower posterior corner of the ischium; it is usually attached to the ischium but seldom shows any connection to the anterior part of the pubis. In *Aquila* the pubis may or may not form a complete ventral border for the obturator foramen. I found no pubic elements posteriorly in *Aquila.* The cathartid pubis is complete and extends past the distal end of the ischium for some distance. The caudal end turns medially in a gentle curve toward the cloacal region. No instances of fusion of pubis and ischium were found in the vultures; they are connected only by strong ligaments and fascia.

Shape of the ilio-ischiatic foramen is quite variable among the genera (plate 10). In the Accipitridae the posterodorsal border is largely flattened out and widened by a strong flange of the ilium that extends medially and anteriorly to fuse with the transverse process of the last vertebra in the pelvis. Because the flange of the ilium extends directly medially and not anteriorly, the borders of the foramen in *Coragyps* and *Cathartes* are left intact; due to a slight anterior direction of the flange in *Gymnogyps, Vultur* and *Sarcoramphus* part of the posterior border is deleted. This flange provides a brace strengthening the postacetabular region.

The point just ventral to the acetabulum, where the ilium, ischium and pubis fuse is greatly strengthened by an enlargement in the Accipitridae. Although traces of this expansion are visible in all the cathartids, it is best developed in *Coragyps.* Increase in size in this region provides a wider articulating surface on the floor of the acetabulum and greater strength. The body weight is supported on the roof of the acetabulum, but the floor of the acetabulum is the region supporting the leg when it is raised from the ground or used independently in preening, tearing food or carrying prey. The widening provides for better support of the limb and a greater variety of movements. It may be termed an adaptation correlated with more extensive use of the hind limb, whether that use is in predation as in the hawks or in terrestrial locomotion as in *Coragyps* and *Vultur.* Another feature adding to the sturdiness in the acetabular region in hawks is a

brace between the vertebral column and the upper posterior corner of the acetabulum immediately medial to the antitrochanter. The brace is formed by processes running laterally from the third and fourth from the last fused vertebra. Occasionally the fifth vertebra from the caudal end also sends a slim process laterally. In cathartids the processes are present but do not extend as far laterally and thus offer less support.

The antitrochanter is heaviest and longest in the Accipitridae. However, it is more highly developed in *Coragyps* and *Vultur* than in *Gymnogyps*, *Cathartes* and *Sarcoramphus*. A major difference is the increased bearing surface of the acetabular ring in the hawks. In *Coragyps* the articulating area is somewhat larger than in the other cathartids.

TABLE 27.—Average Length of Bones in Millimeters.

	Femur	Tibia	Fibula	Tarsus
Gallus	84.6 (4)	120.6 (4)	88.5 (4)	81.8 (4)
Pandion	79.6 (12)	126.6 (10)	103.1 (6)	54.0 (12)
Aquila	127.4 (12)	168.8 (12)	123.1 (10)	104.6 (12)
Cathartes	69.8 (16)	119.3 (13)	83.6 (14)	64.5 (14)
Coragyps	85.8 (8)	141.5 (7)	100.5 (6)	82.0 (8)
Gymnogyps	138.5 (8)	210.0 (5)	144.5 (3)	114.7 (6)
Sarcoramphus	100.0 (4)	165.0 (4)	115.0 (4)	99.0 (4)
Vultur	153.1 (4)	243.0 (4)	158.0 (2)	130.1 (4)

FEMUR

As seen in table 27 *Vultur* has the longest femur (153 mm.) and *Cathartes* the shortest femur (69.8 mm.) of all the forms examined. Table 28 shows, however, that in relation to trunk length and leg length the femora of the cathartids, except *Cathartes*, are about equal in length. Further, all have shorter femora than *Gallus*. The smallest ratios of diameter to length indicate that the femur is relatively sturdy in all the New World vultures, but it is of interest that *Coragyps*, and to a lesser extent *Vultur*, approach the condition demonstrated by *Gallus*, a walking or somewhat cursorial bird. Proximally, the width (through head and trochanter) of the femur in *Coragyps* is less than in other vultures. Distal width (through condyles) is less variable, but again *Coragyps* is nearer to *Gallus* than is any other cathartid.

TABLE 28.—Ratios Concerning the Femur.

Ratio	Gallus	Pandion	Aquila	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Femur: trunk	78.3	70.4	72.0	56.3	61.3	63.6	62.9	60.3
Femur: leg	24.1	24.3	25.8	20.9	21.5	23.7	21.7	23.0
Proximal width: length	19.1	20.1	21.3	24.3	20.9	22.7	22.7	23.9
Distal width: length	19.6	20.1	23.5	24.9	24.0	25.1	25.3	25.3
Smallest diameter: length	8.1	8.5	9.4	11.9	9.8	11.3	11.6	10.5

On first sight few outstanding structural variations in the femora are visible, but careful examination reveals several significant differences (plate 11). In lateral view the shaft in *Gallus* is bowed anteriorly to a greater degree than in any other genus examined, with the possible exception of *Coragyps*. Note the straightness of the shaft in *Cathartes* and *Vultur*. Another important difference is that in *Gallus*, and to a lesser extent in *Coragyps*, the distal end appears to be rotated inward in such a manner that the distal segments of the limb are directed more toward the median line. The rotation

is not evident in the other cathartids, in *Pandion* or in *Aquila*. Much the same result, however, is produced in *Gymnogyps* and *Sarcoramphus* by a medial bending of the condylar region. In *Pandion* the bending is greatest, perhaps to approximate the feet in seizing prey. *Cathartes* and *Vultur* show little bending but no rotation. Thus far in the discussion it might be concluded that in the cathartids, except *Cathartes* and *Vultur*, the lower leg would be directed in approximately the same manner, However, in *Vultur* and *Coragyps* the rotular groove is displaced farther medially than in the other vultures. Then too, in *Gallus* and *Coragyps* the distal two-thirds of the femur is turned medially by a slight bend between the first and second thirds of the shaft. Thus, listed in the order of decreasing medial displacement of the distal end of the femur, the genera would stand as follows: *Pandion*, *Gallus*, *Coragyps*, *Vultur*, *Gymnogyps* and *Sarcoramphus*, *Cathartes* and *Aquila*.

Any feature of the femur, rotation or displacement of condyles or bending of the shaft, that tends to direct the lower leg medially is an important modification since it indicates a trend toward elimination of a straddling walk. Drawing of the legs beneath the body and toward the midline is an adaptation to better terrestrial locomotion and to a better mechanism for predation. In *Pandion* the feet are used together in catching fish. Usually the talons grasp the fish side by side; digit II of one foot may even overlap the same digit on the other foot.

The rotular groove is widest in *Gallus*. *Coragyps* and *Vultur* have the widest grooves of any cathartids. Depth of the groove is greatest in *Pandion* and *Gallus*, but the deep rotular grooves of *Vultur* and *Sarcoramphus* are noteworthy. *Gallus* possesses high ridges on the edges of the rotular groove; proximally they end abruptly on the anterior face of the shaft. In *Vultur* and *Coragyps* the ridges are lower than in *Gallus* but higher than in *Cathartes*, *Sarcoramphus* and *Gymnogyps* in which the rotular ridges are low and rounded and merge gradually into the shaft. On plate 11 note the high rotular ridges of *Pandion* and *Aquila*. The attachments for the flexor muscles on the external condyle are best developed in *Pandion* and *Aquila* as would be expected, but among the vultures they are more manifest in *Coragyps* and *Vultur*. The fibular groove is deepest in *Gallus*, *Coragyps* and *Cathartes* and is shallowest in *Gymnogyps*, *Vultur* and *Sarcoramphus*. In *Pandion* the fibular condyle is fused distally with the internal condyle to form a broad, smooth articulating surface.

Wide, deep rotular and fibular grooves with high ridges bordering them are associated with dexterity of movement of the lower leg, since they aid in the prevention of dislocations of the bones and of the tendons passing over the knee. These features are well shown in *Pandion* and *Aquila* where they contribute to the formation of the mechanism of predation. The same features in *Gallus* are associated with walking and running ability. Thus it is significant that *Coragyps* and *Vultur* show more of these characteristics of structure than do the other cathartids.

The anterior intermuscular line (plate 11) marks the boundary between the origins of Mm. vastus lateralis and vastus medialis. In *Gallus* it extends diagonally across the femoral shank from the trochanteric ridge to the internal femoral condyle. In all cathartids except *Coragyps* it arises medial to the ridge, runs to the distal end of the ridge and then down the shaft toward the internal condyle. The length of the line is greatly variable in the cathartids, but as a rule it extends to the condyle in *Coragyps* and *Sarcoramphus* and is shorter in the other genera. Apparently in the vultures the proximal extent of the origin of M. vastus medialis is limited by the presence of a large pneumatic fenestra on the medial side of the trochanteric ridge. Yet, in *Coragyps* the position of the line is similar to that in *Gallus* and *Pandion*. The placement of this line is of interest in differentiating the femora, but is of little significance from an adaptional viewpoint. The vastus muscles on either side of the line are inseparably fused in the Cathartidae and perform the same function.

In *Gymnogyps* the popliteal area is similar in width but shallower than in *Vultur* and *Sarcoramphus*. *Gallus* shows the narrowest area, but it is no deeper than in *Coragyps* and *Cathartes* in which the area is relatively wider. In *Pandion* the popliteal area is very deep, but *Aquila* has a broad, shallow popliteal area. Although depth of the popli-

teal area has in the past been correlated with development of the various toe flexors which originate here, such a correlation is not always present as for example in the great difference between *Pandion* and *Aquila*.

The intercondylar fossa is slight in *Gallus* and the cathartids; no differences are visible. It is deep in *Aquila* and even deeper in *Pandion*.

TIBIOTARSUS

In absolute values, *Vultur* has the longest tibia and *Cathartes* the shortest (table 27). Ratios of tibial length to trunk, leg and femoral lengths (table 29) show that relatively *Sarcoramphus* has the longest tibia; *Coragyps* and *Vultur* have tibiae of about the same relative lengths, but shorter than in *Sarcoramphus*. In *Cathartes* and *Gymnogyps* the tibiae are short and of about equal length. The high ratio of tibia to femur in *Cathartes* is due to its short femur, and the low ratio for *Gymnogyps* is caused by its longer femur. It is significant that all the tibia to leg length ratios except that for *Pandion* are about the same. The longer tibia in *Pandion* is probably an adaptation to its method of capture of fish.

Using the width through the internal and external articulating surfaces as the proximal width of the tibia, the proximal width to length ratios indicate few definite differences. Larger articulating areas are often associated with a graviportal adaptation to bear heavy weights. There is an indication of such adaptation in the values given for the cathartids, but one must conclude that *Vultur*, the largest cathartid, shows it least of all. Distally the tibial width through the malleoli is least in *Coragyps* and greatest in *Gymnogyps* and *Sarcoramphus*.

In all the cathartids and in *Gallus* the tibia bends posteriorly. This bend is greatest in *Cathartes* and *Vultur* and least in *Coragyps* and *Gymnogyps*. The effect of this bend in *Gallus*, *Coragyps*, *Cathartes* and *Vultur* is, however, largely counteracted by a bend anteriorly just above the malleoli. Thus in *Vultur*, *Gymnogyps*, *Aquila*, *Sarcoramphus* and *Cathartes* the tibiae are functionally almost straight. In *Gallus* and *Pandion* the malleoli are displaced forward. There is some anterior displacement in *Coragyps*.

TABLE 29.—Ratios Concerning the Tibia.

	Gallus	*Pandion*	*Aquila*	*Cathartes*	*Coragyps*	*Gymnogyps*	*Sarcoramphus*	*Vultur*
Tibia: trunk	111.7	112.0	95.4	96.0	101.0	96.8	104.0	100.0
Tibia: leg	34.4	38.6	34.2	35.7	35.4	35.9	35.8	36.6
Tibia: femur	143.0	159.0	133.0	170.0	165.0	152.0	165.0	164.6
Fibular crest: tibia	16.1	27.3	21.5	19.7	19.5	21.5	22.4	20.3
Proximal width: length	12.1	10.6	13.7	11.4	11.6	13.0	12.1	12.0
Distal width: length	10.7	11.4	13.2	10.4	9.5	11.6	11.3	10.6

Other features of the tibiotarsus are similar in all the cathartids with few exceptions. The inner cnemial crest in *Coragyps* is relatively small. The proximal part of the inner cnemial crest is directed somewhat externally in *Vultur*, *Sarcoramphus* and *Cathartes* and to a lesser degree in *Coragyps*. The entire crest, using the distal end as a pivot, is swung outward in *Gallus* and *Sarcoramphus*. This inner crest nearly parallels the shaft in *Gymnogyps* and *Cathartes*, but only the distal part of the crest does so in *Gallus* and *Coragyps*. The malleoli of the tibia are displaced medially only in *Coragyps* among the vultures.

The median condyle or malleolus in *Gallus*, *Cathartes* and *Vultur* is wider anteroposteriorly than the external condyle. In the other cathartids the malleoli are essentially equal in this respect. The external malleolus is longer than the internal malleolus in all the genera except *Pandion* and *Aquila* where the reverse is true. The external malleolus is larger in *Gymnogyps* than in *Vultur*.

Supratendinal bony bridges for the M. extensor digitorum longus are similar in the cathartids, but *Gymnogyps* has the narrowest bridge. No differences among the vultures could be observed in the tendinal groove for M. extensor digitorum longus, but in them it extends farther up the shaft than in *Gallus* or in *Aquila*.

As suggested previously, the tibiotarsi of vultures show little differentiation, but the tibia of *Coragyps* most closely approaches that of *Gallus*.

FIBULA

Table 30 shows only small variations in fibular lengths, but in the discussion of the tibiotarsi it was shown that the tibiotarsus was proportionately longest in *Sarcoramphus*. Thus *Sarcoramphus* also has the longest fibula. *Coragyps* has a longer fibula than *Cathartes* and *Gymnogyps*, and *Vultur* possesses the shortest fibula of all. Length of the fibular spine is of importance since M. peroneus brevis and M. flexor perforans et perforatus digiti III use the spine for a major part of their origins. In fact, the distal extent of their origins usually corresponds to the distal extent of the fibular spine.

TABLE 30.—Ratios Concerning the Fibula.

	Gallus	Pandion	Aquila	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Length: tibia	73.4	81.4	72.9	70.1	71.0	69.0	69.7	64.9
Breadth of head: length	10.4	8.1	12.5	10.6	10.8	12.2	11.8	12.5
Thickness of head: length	30.1	48.7	36.7	39.3	41.7	37.7	38.2	40.3

Anteroposterior length of the articulating surface of the head of the fibula is greatest in *Aquila*, *Vultur* and *Gymnogyps*, and is only slightly less in *Sarcoramphus*. In this respect *Cathartes* and *Coragyps* agree closely with *Gallus*. Thickness of the fibular head is greatest in *Pandion*, but *Coragyps* and *Vultur* present somewhat greater size than do the other cathartids. Considering both length and width the articulating area of the fibula is smallest in *Gallus*, with *Cathartes*, *Coragyps* and *Pandion* in an intermediate group. The area is largest in *Vultur* but is only slightly smaller in *Gymnogyps*, *Sarcoramphus* and *Aquila*. Size of the articulating surface appears to be correlated with the weight of the bird.

The spine of the fibula is not fused to the tibia in *Gallus* but continues as a ligament almost to the external ligamental prominence. In the other forms examined the tip of the spine is more or less fused with the tibia; this is more pronounced in *Pandion*. Shufeldt (1909:49) noted that the distal end of the fibula in the cathartids terminates in a free, pointed end, but adds, "the union is very intimate . . . in the skeleton of *Sarcoramphus*." [Vultur]. Throughout its length the fibula is heaviest in *Vultur*.

TARSOMETATARSUS

In relation to trunk, leg, femoral and tibial lengths the tarsus is longest in *Gallus*. Of the vultures *Sarcoramphus* possesses the longest tarsus, but it is not much longer than in *Coragyps*. Relative tarsal lengths are approximately equal in the other New World vultures (table 31).

Ratios of distal width to length and of proximal width to length indicate that of the cathartids *Coragyps* has tarsal proportions most closely approaching those of the chicken. *Cathartes* is next closest with *Sarcoramphus*, *Vultur* and *Aquila* following in that order. Only in *Pandion* do the ratios exceed those in *Gymnogyps*. The tarsal shaft is relatively widest in *Gymnogyps* and *Cathartes* and is narrowest in *Gallus* and *Coragyps* with *Vultur* and *Sarcoramphus* in an intermediate group. Miller (1911) gives the series from broad to narrow tarsus as *Cathartes*, *Gymnogyps*, *Vultur* and *Coragyps*. In 1910 the same author observed that the tarsus is markedly flattened in *Cathartes*, *Sarcoramphus* and *Gymnogyps*, that the difference between the tarsi of *Gymnogyps* and *Vultur* is almost entirely one of relative width, and that the width of the shaft varies with age. Round tarsi, as found here in *Gallus*, *Coragyps*, and to a lesser degree in *Vultur*, are most frequently found in forms adapted for swift walking or running. Miller (1912: 86) found a more robust tarsus, absolutely and relatively, in fossil cathartids. Especially was this true in the black vulture. The slim, round tarsus now found in *Coragyps* is thus a modification toward better locomotion on the ground. It is interesting to note that he (Miller) found no structural differences between Recent and fossil tarsi of the California condor except larger size in the fossil tarsi. He also states that the size of the tarsus in *Cathartes* is subject to considerable variation.

TABLE 31.—Ratios Concerning the Tarsometatarsus.

	Gallus	Pandion	Aquila	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Tarsus: trunk	75.7	47.8	59.1	52.0	58.6	53.0	62.3	51.5
Tarsus: leg	23.3	16.5	21.2	19.3	20.5	19.6	21.5	19.6
Tarsus: femur	96.9	67.8	82.4	92.4	95.6	83.3	99.0	85.3
Tarsus: tibia	67.8	42.5	61.9	54.2	57.9	54.8	60.0	53.6
Proximal width: length	17.4	27.4	22.4	21.2	18.7	23.1	20.5	22.1
Distal width: length	18.3	28.3	24.4	24.2	20.6	25.6	23.8	23.3

In *Pandion*, a single, large tendinal canal is formed by the calcaneal ridges on the hypotarsus (plate 12, fig. e). One or two covered canals and one or two uncovered canals are present in *Gallus*. None of the cathartids possess roofed canals in the hypotarsus; only flat depressions are present, and I could see no differences in the degree of depth or width. However, Shufeldt (1909:50) describes a sharp, vertical groove in the hypotarsus of *Cathartes* and *Coragyps* and a broad, shallow concavity in the rest of the New World vultures.

The internal calcaneal ridge in the cathartids extends medially and forms a shelf-like extension giving greater width to the surface supporting the flexor tendons passing over the hypotarsus. This is most pronounced in *Gymnogyps* and is least in *Coragyps* and *Cathartes*. However, only in *Gymnogyps*, and to some extent in *Vultur*, does the external calcaneal ridge form an extension laterally. These extensions of the bearing surface for the tendons crossing the hypotarsus are modifications for better support and for better maintenance of the position of the tendons; this is especially true in birds which possess incomplete canals only. *Aquila* has well developed median and lateral calcaneal ridges which form a deep trough (plate 12).

The protuberance for the insertion of the M. tibialis anterior is 19 per cent of the way down the tarsus in *Gymnogyps* and *Vultur*, 18 per cent in *Sarcoramphus*, 16.6 per cent in *Gallus*, 14.9 per cent in *Cathartes* and 13.9 per cent in *Coragyps*. In *Aquila* the insertion is 23.8 per cent of the way down the tarsus, and it is 34.1 per cent in *Pandion*. Miller (1912:93) has found that the papilla for the insertion of the M. tibialis anterior is more proximal in long, narrow tarsi and is more distal in shorter heavier tarsi. This is in agreement with the figures just given. The more distal insertion in the latter two serves to increase the power to flex the tibiotarsal joint and to raise the foot. Two

factors that enter into the placing of the insertions are power and speed of flexing the joint. A more proximal insertion as in *Coragyps* gives greater speed but less power. This may be correlated with a running or walking foot. The significance of the insertion point will be discussed further in connection with the M. tibialis anterior.

The elevated inner border of the anterior face of the tarsus disappears distally and gives the impression that the distal end of the tarsus is rotated inward. This modification is most extreme in *Pandion* and *Aquila*, producing a triangular cross section. *Coragyps*, *Gymnogyps*, *Sarcoramphus* and *Vultur* show this character to a small degree, but in *Cathartes* the inner and outer borders are similarly developed.

The trochlea for digit II is most proximal and posterior in *Gallus* and the articular end faces in toward the median line. In the other genera, except *Pandion*, the trochlea is more distal; in *Gymnogyps* and *Vultur* it is more proximal than in the other vultures. Shufeldt (1909:50) described the three trochlea of *Coragyps* as lying nearly in the same transverse plane. See plate 12, fig. *g* to observe the incorrectness of this statement. *Pandion* shows the extreme of this medial turning. The wing of the trochlea for digit II is similarly developed in the Cathartidae; it is much larger in *Pandion* in which it is directed posteriorly. In *Aquila* the wing is large but runs medially and somewhat posteriorly. The wing serves to hold in place the tendons of the muscles flexing digit II.

The middle trochlea (for digit III) is in line with the sagittal axis of the tarsometatarsus in all the vultures except *Coragyps;* in this genus it is placed farther medially as in *Gallus* (plate 12, figs. *f* and *g*). Note that in *Aquila* the trochlea turns laterally!

In all the genera except *Aquila* the fourth metatarsal trochlea lies proximal to the third trochlea. It is most proximal in *Gallus*, *Coragyps*, *Pandion* and *Cathartes*. This trochlea faces most laterally in *Pandion* and *Aquila;* thus the longitudinal axis of digit IV almost corresponds to the transverse axis of the foot as a whole. In *Gallus* the fourth toe lies more laterally than in the cathartids. *Coragyps*, *Cathartes* and *Vultur* approach the condition in the chicken more than do *Gymnogyps* and *Sarcoramphus*. On the outer edge of the trochlea for digit IV a wing projects posteriorly. This development to hold the flexor tendons in place is best seen in *Pandion* and *Aquila*. The vultures have a relatively small wing, about equal to that on trochlea 2, but *Gallus* possesses a larger wing.

Significant features of the tarsus in the New World vultures are: its great length in *Sarcoramphus* and *Coragyps;* the similarity in the strength of the bone in *Coragyps* and *Gallus* and the greater width in *Cathartes* and *Gymnogyps;* the shelflike extensions of the calcaneal ridges; the more distal insertion of M. tibialis anterior in *Gymnogyps*, *Vultur* and *Sarcoramphus;* trochlea 2 faces more medially in *Coragyps* and *Vultur* than in the other cathartids; trochlea 3 is placed farthest medially in *Coragyps;* trochlea 4 is most posteriorly located in *Coragyps* and *Cathartes*, and in this regard the condition is similar to that in *Gallus;* the fourth trochlea faces most laterally in *Coragyps*, *Cathartes* and *Vultur*.

In the instances of variation within the Cathartidae, *Coragyps* and *Vultur* show more similarity to *Gallus* than do the other vultures, but *Sarcoramphus* shows more likeness to the chicken than do *Cathartes* and *Gymnogyps*. Greater length of the tarsus as in *Sarcoramphus* and *Coragyps* is without doubt an adaptation for better cursorial locomotion; increased length in the ankle bones has been shown to be correlated with increased speed of ground locomotion in many animals. The similarity of internal proportions of the tarsus in *Coragyps* and *Gallus* indicates a cursorial adaptation in the black vulture; the roundness of the tarsus of *Gallus*, *Coragyps*, *Vultur* and *Sarcoramphus* is a feature usually associated with a proclivity for swift terrestrial locomotion.

The position assumed by the digital trochlea is significant. In the foot designed for predatory activities (*Pandion* and *Aquila*) the first and fourth toes are directed posteriorly to a great extent; the effect is to cause each talon to approach the object to be seized from a different direction. Thus there is less chance for the prey to slip between the talons. In the species which are relatively heavy and which possess tendencies toward

a graviportal stance the toes may be spread to create a wider base to aid in balancing the weight. In *Vultur* the length of the first and fourth toes is reduced; this decreased length as an adaptation for better locomotion reduces the modifications in the trochleae for these toes. That is, the toes are being lost in place of being modified for better support. However, in *Gymnogyps*, a bird of similar weight, the toes are not reduced as much, and are more widely spaced for better balance.

METATARSAL I

As may be observed in table 33, metatarsal I is approximately the same absolute length in *Gallus*, *Coragyps* and *Cathartes* and about the same in *Vultur*, *Sarcoramphus* and *Gymnogyps*. Only on the basis of details of structure may the members of either group be distinguished. However, table 32 shows that metatarsal I is relatively longest in *Gallus*, *Cathartes* and *Sarcoramphus* and is shortest in *Vultur*. In *Gymnogyps* it is considerably longer than in *Vultur* but is of about the same length as in *Coragyps*.

In *Cathartes* the digital condyle is symmetrical and as a consequence digit I tends to project straight posteriorly. In the other genera the condylar surface is inflated on the outer edge and is wider, thus allowing for more movement of the digit, especially for medial deflection, and making a better bearing surface. Proximally the first metatarsals of *Gallus*, *Coragyps* and *Vultur* are of greater width and therefore provide for better attachment to the tarsometatarsus. The facet lies on the inner posterior corner of the tarsus in the cathartids, but in *Gallus* it is almost entirely on the posterior surface. Articulation with the tarsus is the same in all cathartids—by means of an elongated, slightly inflated head that is somewhat rounded. In *Gallus* and *Pandion* the articulating surface is elongate, lies essentially in a straight line and is not rounded.

The internal surface of the first metatarsus above the digital condyle is hollowed out in such a way in *Pandion* that a complete bony sheath is formed for the flexor tendons; the tarsometatarsus provides the anterior half of the bony circlet. The digital condyle is deeply grooved distally on its inner surface for the passage of the Mm. flexor hallucis tendons. In none of the other genera are the extreme excavation and grooving of the internal surface visible. Only in *Cathartes*, and perhaps *Coragyps*, of the vultures is the digital condyle noticeably grooved distally. *Vultur* shows the least concavity above the condyle. A well developed cavity provides a canal for the passage of tendons to the first phalanx. This condition is best exhibited by predaceous birds using the digits as grasping organs and by perching birds. It is of interest that in *Cathartes* and *Coragyps* traces of it may be seen. In *Gymnogyps* and *Vultur* the distal groove is practically nonexistent. *Sarcoramphus*, in this respect, is intermediate between *Coragyps* and *Gymnogyps*.

The important features of the first metatarsals in the Cathartidae are: the long, posteriorly-directed metatarsal in *Cathartes;* the very short bone, lacking any concavity, in *Vultur;* the strong attachment to the tarsometatarsus in *Gallus*, *Coragyps* and *Vultur;* the sturdiness in *Gymnogyps;* and the grooving of the digital condyle in *Cathartes* and *Coragyps*.

Digit I.—*Vultur has* a much shorter digit I than any other genus examined (table 32). Only in the ratios of digit I to digit IV and of digit I to tarsus is there apparent evidence to the contrary, and it has previously been shown that *Gallus* has a much longer tarsus. Digit IV is also longer in *Gallus* than in *Vultur*. Digit I in *Gymnogyps* is appreciably longer than in *Vultur* and *Gallus* but is about the same length as in *Coragyps*. *Sarcoramphus* possesses the longest digit, but it is not much longer than in *Cathartes*.

Analysis of the second part of table 32 demonstrates that the short digit in *Vultur* is due primarily to a reduced phalanx 1; approximately the same condition exists in *Gymnogyps* except that phalanx 1 is relatively longer. Thus these two vultures approach the phalangeal lengths of *Aquila* and *Pandion*. Relative lengths of the phalanges of digit I are about the same in *Cathartes* and *Sarcoramphus*, and in *Gallus* and *Coragyps*. In these four genera phalanx 1 constitutes more than 60 per cent of the digit length.

Phalanx 1 is more robust in *Gymnogyps* and *Pandion*, but in *Vultur* it is heavier than in the other genera, except *Aquila*. It is arched dorsally in all forms except *Gymnogyps* and *Vultur* in which two it is practically straight. The groove for the flexor tendons is well developed in *Cathartes* and *Coragyps* and is just barely visible in *Gallus* and the remaining cathartids. Condyles for the ungual phalanx are equally developed in the vultures and are stronger than in *Gallus*.

No significant differences in the curvature of the claw were observed among the Cathartidae. The curvature may be somewhat less in *Cathartes* and *Sarcoramphus*. The flexor attachment on the claw is best developed and is longest in *Coragyps* and *Sarcoramphus* of the cathartids.

TABLE 32.—Ratios Concerning Digit I.

	Gallus	Pandion	Aquila	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Length: trunk	21.0	41.0	42.6	22.2	20.5	19.1	23.1	16.0
Length: leg	6.4	14.1	15.3	8.2	7.2	7.1	8.0	6.1
Length: femur	26.8	58.2	59.3	39.4	33.4	20.0	36.7	26.5
Length: digit II	56.4	87.0	87.7	61.0	52.0	51.4	55.3	47.0
Length: digit III	36.3	75.8	85.9	46.6	32.4	32.7	37.7	28.6
Length: digit IV	41.0	81.0	109.0	52.1	49.0	45.8	47.2	45.1
Length: tarsus	27.7	85.7	72.2	42.6	35.0	36.9	37.1	31.1
Length: tibia	18.8	36.6	44.7	23.0	20.3	19.8	22.2	16.6
Metatarsal I: tarsus	13.9	30.4	24.5	18.3	14.1	14.7	16.0	12.6
Metatarsal I: digit I	50.2	35.4	34.0	42.9	40.4	40.5	42.7	40.3
Phalanx 1: digit I	61.2	50.1	51.6	63.6	62.0	56.8	63.2	52.2
Phalanx 2: digit I	38.7	49.9	48.3	36.3	38.0	43.1	36.8	47.8
Phalanx 1: tibia	11.4	18.3	23.1	14.7	12.5	11.2	14.1	8.7
Phalanx 2: tibia	7.3	18.5	21.6	8.4	7.7	8.5	8.2	8.0
Phalanx 1: phalanx 2	158.0	100.0	107.0	175.0	163.0	132.0	172.0	110.0
Phalanx 2: phalanx 1	63.3	100.0	93.6	57.1	61.2	75.8	58.2	91.4

Significant variations in digit I are: (1) its shortness in *Vultur* and to a lesser extent in *Gymnogyps*, due chiefly to a much shorter phalanx 1, (2) the great similarity in digital and phalangeal lengths in *Gallus* and *Coragyps*, (3) the sturdiness of the bones and the absence of any arching in phalanx 1 in *Gymnogyps* and *Vultur*, (4) the development of the flexor grooves in *Cathartes* and *Coragyps*, and (5) the longer and stronger flexor attachments in *Coragyps* and *Sarcoramphus*.

Although *Vultur* and *Gymnogyps* have been grouped together it is obvious that neither the shortness of the digit as a whole nor the shortness of phalanx 1 is as apparent in the California condor. Heavier phalanges and absence of arching in phalanx 1 is probably correlated with the greater weight of these two birds. That digit I in *Vultur* is significantly weaker than in any other cathartid is shown not only by its proportions just discussed but also by the short, poorly developed first metatarsal and, as will be discussed later, by the weak musculature.

TABLE 33.—Average Length in Millimeters of Digit I.

	Metatarsal	Phalanx 1	Phalanx 2	Total
Gallus	11.4 (4)	13.9 (4)	8.8 (4)	22.7
Pandion	16.4 (12)	23.2 (12)	23.1 (12)	46.3
Aquila	25.7 (10)	39.0 (11)	36.5 (10)	75.5
Cathartes	11.8 (15)	17.5 (15)	10.0 (12)	27.5
Coragyps	11.6 (7)	17.8 (8)	10.9 (8)	28.7
Gymnogyps	16.8 (3)	23.6 (3)	17.9 (3)	41.5
Sarcoramphus	15.7 (3)	23.2 (3)	13.5 (3)	36.7
Vultur	16.3 (2)	21.2 (4)	19.3 (4)	40.5

Digit II.—Digit II shows less variation in length than digit I. It is shortest in *Vultur*, but it is perhaps only insignificantly shorter than in *Cathartes* and *Gymnogyps*. In *Coragyps* it is longer than in the latter two cathartids. In *Sarcoramphus* it is decidedly longer. It is of interest that the ratios for the chicken fall approximately in the middle of the cathartid range. In analyzing the ratios in table 35, it should be remembered that the segments of the hind limb are relatively long in *Gallus*. This accounts for the lower ratios for digit II of the chicken.

TABLE 34.—Average Length in Millimeters of Digit II.

	Phalanx 1	Phalanx 2	Phalanx 3	Total
Gallus	14.4 (4)	14.5 (4)	11.3 (4)	40.2
Pandion	9.8 (11)	19.9 (12)	23.5 (12)	53.2
Aquila	14.9 (8)	30.5 (12)	40.7 (6)	86.1
Cathartes	15.3 (16)	13.6 (15)	16.2 (15)	45.1
Coragyps	21.6 (8)	18.2 (8)	15.4 (8)	55.2
Gymnogyps	30.6 (3)	24.8 (3)	25.3 (2)	80.7
Sarcoramphus	21.6 (3)	23.5 (3)	21.3 (3)	66.4
Vultur	34.1 (4)	25.6 (4)	26.6 (4)	86.3

The second part of table 35 shows that in *Vultur* the shortness of digit II results from shorter phalanges 2 and 3. Phalanx 1 is as long, if not longer, than that of any other genus. In *Gymnogyps* all phalanges are reduced but especially phalanges 2 and 3. In *Cathartes* it is phalanges 1 and 2 which are shorter; the claw is longer than in other cathartids. *Coragyps* exhibits a gradient of decreasing length from phalanx 1 to phalanx 3. The phalanges are of more equal length in *Sarcoramphus* but the greater length of the digit is a result of the greater length of phalanx 2. Phalanx 3 is a little longer, but phalanx 1 is a great deal shorter than in other cathartids, except possibly in *Cathartes*.

In the walking foot as exemplified by the chicken, phalanges 1 and 2 are about equal in length, and the claw is shorter. In the foot of predatory birds (*Pandion* and *Aquila*) the proximal phalanx of digit II is about one-half as long as phalanx 2 and is much less than half as long as the claw. I fail to see in the digit II of cathartids any striking resemblance to either type. The claw in *Coragyps* constitutes the same per cent of the digit as in Gallus; it is much longer, however, in *Cathartes*. Phalanx 2 contributes about the same part of the digit in *Gallus*, *Pandion*, *Aquila* and *Sarcoramphus*. This phalanx apparently has not been modified as much as phalanges 1 and 3. (See ratios of phalanx 2 to digit II and the three ratios of phalanx to tibia.)

Considering both the extramembral and the intradigital ratios I think that *Coragyps* exhibits the greatest similarity to *Gallus* as regards digit II. The longer phalanx 1 is the principal dissimilarity, and the difference there is only about 3 per cent.

It is worthy of notice that although there is only a slight variation in the length of digit II in cathartids this variation may be the result of modification of any one of the three phalanges. However, variation in length, at least in the cathartids, is most common in phalanx 3 and is least common in phalanx 2 of digit II.

The phalanges of digit II are slimmest in *Coragyps* and *Gallus* and most robust in *Vultur* and *Gymnogyps*. Phalanx 1 is arched dorsally in *Cathartes* and *Coragyps*, and

TABLE 35.—Ratios of Digit II.

	Gallus	Pandion	Aquila	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Length: trunk	37.2	59.6	48.6	36.4	39.4	37.2	41.8	34.1
Length: leg	11.4	16.2	17.5	13.5	13.8	13.8	14.4	13.0
Length: femur	47.5	66.8	67.7	64.6	64.3	58.5	66.4	56.5
Length: tibia	33.3	42.0	51.0	37.8	39.0	38.4	40.2	35.5
Length: tarsus	49.1	98.5	82.3	69.9	67.3	70.2	67.1	66.2
Length: digit I	177.0	115.0	114.0	164.0	192.0	194.0	181.0	213.0
Length: digit III	63.4	77.9	93.3	57.1	60.5	63.5	68.2	60.8
Length: digit IV	73.0	93.0	124.0	85.6	93.5	89.2	85.3	95.9
Phalanx 1: length	35.8	18.4	17.3	33.9	39.1	37.8	32.5	39.5
Phalanx 2: length	36.0	37.4	35.4	30.2	32.9	30.6	35.4	29.7
Phalanx 3: length	28.1	44.2	47.3	35.9	27.9	31.2	32.1	30.9
Phalanx 1: tibia	12.0	7.7	8.8	12.9	15.3	14.6	13.1	14.0
Phalanx 2: tibia	12.1	15.7	18.0	11.4	12.8	11.8	14.2	10.6
Phalanx 3: tibia	9.3	18.5	24.1	13.6	10.8	12.0	12.1	11.0
Phalanx 2: phalanx 1	100.0	203.0	205.0	88.9	84.2	81.0	108.8	75.2
Phalanx 3: phalanx 1	78.5	240.0	273.0	105.9	71.3	82.7	99.1	78.5

in these two the condyles and the flexor groove are better developed than in the other cathartids. In phalanx 2 less variation is present; ventral flexor grooves are absent in all the vultures except *Sarcoramphus* and they are minute in it. Thus phalanx 2 is not only stable as regards size variation, mentioned above, but also as regards its configuration. Phalanx 3 is most variable. Its curvature is about the same in the cathartids, but in *Coragyps* it may be inconsiderably straighter and may approach the straightness observed in *Gallus*. Of the cathartids *Cathartes* shows the greatest possible leverage for the flexor attachments, but the attachment process is smooth. *Sarcoramphus* and *Coragyps* exhibit strong insertions with fair leverage, and *Vultur* shows the poorest attachment of all. The latter resembles that of the chicken. The proximal articulations vary little in cathartids except that those in *Coragyps* and *Sarcoramphus* may be judged stronger if the greater height and sharpness of the interarticular area (as seen in *Pandion*) are used as criteria.

Digit III.—Digit III is longest in *Cathartes*, but it is perhaps unimportantly shorter in *Coragyps* (table 36). *Vultur* possesses a somewhat shorter third toe than *Gymnogyps*. In respect to this toe *Sarcoramphus* is intermediate. The ratios of digit III to leg length reveal that as part of the functional limb digit III is approximately the same length in *Coragyps*, *Gymnogyps*, *Sarcoramphus* and *Vultur*. In *Cathartes* it is significantly longer. Note that in *Gallus* digit III is more abbreviated than in any vulture.

The greater relative length of digit III in *Cathartes* and *Coragyps* is due principally to longer phalanges 2 and 3, and a longer claw in *Cathartes*. The shorter digit in *Vultur* and *Gymnogyps* is chiefly a result of a short third phalanx.

The ratios of phalanx 1 to digit III in the second part of table 36 indicate that phalanx 1 constitutes about the same part of the length of the digit in *Gallus*, *Cathartes* and *Sarcoramphus*. It makes up a greater part of the length in *Coragyps* and *Gymnogyps* and a still greater per cent in *Vultur*. However, the ratio of phalanx 1 to tibia and the interphalangeal ratios show that phalanx 1 is relatively shorter in *Sarcoramphus* than

in *Gallus* and *Cathartes*. The length of phalanx 2 is remarkably similar in the Cathartidae and in *Gallus*.

Phalanx 2 is longest in *Cathartes* and *Coragyps*. Neither phalanx 1 nor phalanx 2 in the vultures shows the major reduction of length found in the grasping feet of *Pandion* and *Aquila*.

Phalanx 3 forms the same part of digit III in *Gallus*, *Cathartes*, *Coragyps* and *Sarcoramphus*. In *Gymnogyps* phalanx 3 is a smaller part of the digital length. In *Vultur* it is a still smaller segment of the whole. Phalanx 3 is longest and about equal in length in *Cathartes*, *Coragyps* and *Sarcoramphus*. It is significantly shorter and approx-

TABLE 36.—Ratios of Digit III.

	Gallus	*Pandion*	*Aquila*	*Cathartes*	*Coragyps*	*Gymnogyps*	*Sarcoramphus*	*Vultur*
Length: trunk	58.4	59.7	52.1	66.0	64.6	58.5	61.3	56.0
Length: leg	18.0	20.6	18.7	24.5	22.6	21.7	21.1	21.2
Length: femur	74.5	84.7	72.4	117.2	105.4	92.0	97.4	92.8
Length: tibia	52.3	53.2	54.6	68.6	63.9	60.5	59.0	58.4
Length: tarsus	77.1	124.8	88.1	126.8	110.2	110.4	98.4	108.8
Length: digit I	277.0	145.0	122.0	297.5	315.0	306.0	265.0	350.0
Length: digit II	157.0	127.0	107.0	181.0	164.0	157.0	147.0	164.5
Length: digit IV	115.0	118.0	135.0	155.0	153.0	140.0	125.0	158.0
Phalanx 1: length	31.7	22.6	29.8	31.7	33.3	33.4	30.5	35.2
Phalanx 2: length	24.7	9.1	13.1	24.9	25.2	24.3	24.4	25.4
Phalanx 3: length	23.3	32.5	27.4	22.9	22.7	20.8	23.6	18.8
Phalanx 4: length	20.3	35.7	29.6	20.5	18.8	21.6	21.5	20.5
Phalanx 1: tibia	16.5	12.0	16.3	21.8	21.2	20.2	18.0	20.5
Phalanx 2: tibia	12.9	4.9	7.2	17.1	16.0	14.7	14.4	14.8
Phalanx 3: tibia	12.1	17.2	15.0	15.7	14.4	12.6	13.9	11.0
Phalanx 4: tibia	10.6	19.0	16.2	14.1	12.0	13.1	12.7	13.1
Phalanx 2: phalanx 1	78.0	40.8	44.0	78.8	75.7	72.5	80.3	72.5
Phalanx 3: phalanx 1	73.0	144.4	92.0	72.6	68.1	62.1	77.5	53.6
Phalanx 4: phalanx 1	64.0	158.0	99.3	64.9	56.5	64.7	70.4	58.5

imately equal in *Gallus* and *Gymnogyps*, and is shortest in *Vultur*. Phalanx 4 is the same in *Gallus* and in the cathartids, except for *Coragyps* in which it is a lesser part of the digit and approaches the condition in *Gallus*.

No major differences in the structure of the phalanges of digit III were observed. They are relatively heaviest in the two larger vultures and about the same in the other cathartids and *Gallus*. The phalanges of *Cathartes*, *Coragyps* and *Gallus* are noticeably arched dorsally. Development of the condyles and the proximal articulations is approximately equal in the vultures. In *Gallus* the condyles are much flattened and the proximal articulating surfaces appear weak. Curvature of the claw on digit III is equally greater in the several cathartids than in *Gallus*.

TABLE 37.—Average Length in Millimeters of Digit III.

	Phalanx 1	Phalanx 2	Phalanx 3	Phalanx 4	Total
Gallus	20.0 (4)	15.6 (3)	14.7 (4)	12.8 (4)	63.1
Pandion	15.2 (11)	6.2 (12)	21.9 (12)	24.1 (12)	67.4
Aquila	27.5 (12)	12.1 (10)	25.3 (11)	27.3 (8)	92.2
Cathartes	25.9 (16)	20.4 (16)	18.7 (16)	16.8 (16)	81.8
Coragyps	30.1 (7)	22.8 (8)	20.5 (8)	17.0 (7)	90.4
Gymnogyps	42.5 (3)	30.8 (3)	26.4 (3)	27.5 (3)	127.2
Sarcoramphus	29.7 (3)	23.8 (3)	23.0 (3)	20.9 (3)	97.4
Vultur	49.9 (4)	36.1 (4)	26.6 (4)	29.1 (4)	141.6

Digit IV.—The length of this digit is greatest in *Gallus*, *Pandion* and *Sarcoramphus*. *Vultur* exhibits a significantly short fourth toe; it is shorter by 15 per cent of the body length. In *Coragyps*, *Cathartes* and *Gymnogyps* the length is equal and is intermediate between the length in *Sarcoramphus* and that in *Vultur*. The great length in *Sarcoramphus* is a result of the greater length of all the phalanges but principally of phalanges 2, 3 and 4. In *Vultur* the short toe results from extremely abbreviated phalanges 3 and 4 (table 39).

In absolute values phalanx 1 in the cathartids is longest in *Gymnogyps* and *Vultur* and most closely approximates the length in *Gallus* (table 38). Phalanges 2 and 3 are less variable in all the forms. Phalanx 4 constitutes a greatly variable per cent of the length of digit IV (15.9 in *Vultur* to 34.7 in *Pandion*). *Coragyps*, of the vultures, shows a claw length nearest that of the chicken. Taken as a whole, digit IV of the cathartids possesses phalangeal lengths comparable with those of the chicken. There is no indication of the shortening of proximal phalanges as found in *Pandion* and *Aquila*.

TABLE 38.—Average Length in Millimeters of Digit IV.

	Phalanx 1	Phalanx 2	Phalanx 3	Phalanx 4	Phalanx 5	Total
Gallus	19.1 (4)	9.1 (4)	7.8 (3)	9.1 (4)	9.8 (4)	54.9
Pandion	4.4 (12)	4.7 (11)	4.4 (11)	19.8 (12)	23.7 (12)	57.0
Aquila	15.0 (9)	6.8 (9)	5.9 (9)	19.5 (11)	22.1 (9)	69.3
Cathartes	13.4 (15)	8.3 (16)	7.3 (16)	11.1 (14)	12.6 (13)	52.7
Coragyps	17.1 (7)	9.8 (8)	7.9 (8)	12.1 (8)	12.1 (8)	59.0
Gymnogyps	23.4 (3)	15.6 (2)	13.1 (2)	16.9 (3)	21.5 (3)	90.5
Sarcoramphus	18.5 (3)	14.0 (3)	11.1 (3)	16.5 (3)	17.7 (3)	77.8
Vultur	26.6 (4)	16.0 (4)	11.8 (4)	14.1 (4)	21.5 (4)	90.0

Relative lengths of the phalanges are shown by the ratios of phalanx to tibia and the interphalangeal ratios of table 39. Phalanx 1 is longest in *Coragyps*, but among the Cathartidae the variation is small. Phalanx 2 exhibits little variation; the long phalanx in *Sarcoramphus* is the only significant deviation. The distal phalanges are much more subject to divergence. Note the shortness of phalanx 3 in *Vultur* and *Coragyps* and the greater length in *Sarcoramphus*. Phalanx 4 is shortest in *Vultur* and longest in *Sarcoramphus*. Phalanx 5 is shortest in *Vultur* and *Coragyps* and longest in *Sarcoramphus*.

Summary of Discussion of the Digits

Some of the more significant observations on the digits of the Cathartidae may be listed as follows: (1) Digits I and IV are most variable. (2) Digit I is shortest in *Vultur*, intermediate in *Gymnogyps* and *Coragyps*, and longest in *Cathartes* and *Sarcoramphus*. (3) Digit II is shortest in *Vultur*, *Cathartes* and *Gymnogyps*, intermediate in *Coragyps* and longest in *Sarcoramphus*. (4) Digit III is shortest in *Vultur* with that of *Gymnogyps* only slightly longer, intermediate in length in *Sarcoramphus*, and longest in *Coragyps* and *Cathar-*

tes. (5) Digit IV is by far the shortest in *Vultur,* intermediate in *Coragyps, Cathartes* and *Gymnogyps* and longest in *Sarcoramphus.* (6) Variation in the length of the digits is due for the most part to variation in the distal phalanges, but not always including the ungual phalanx or claw. (7) The morphology of the phalanges in the Cathartidae is similar and shows few important variations. The phalanges are unusually sturdy in *Vultur* and *Gymnogyps* and are slimmest in *Coragyps* and *Cathartes.* The phalanges are more or less arched dorsally in all except *Vultur* and *Gymnogyps. Cathartes* exhibits much the best flexor attachments on the claw. (8) Viewed from all aspects, the digits of *Coragyps* most closely resemble those of *Gallus.*

Relative lengths of the phalanges composing any single digit are reliable indices of the modification of that digit. For example, perching birds as a rule have reduced basal phalanges and lengthened distal phalanges. This modifica-

TABLE 39.—Ratios Involving Digit IV.

	Gallus	Pandion	Aquila	Cathartes	Coragyps	Gymnogyps	Sarcoramphus	Vultur
Length: trunk	50.8	50.0	39.1	42.5	42.1	41.7	48.9	35.5
Length: leg	15.7	17.4	14.1	15.8	14.7	15.5	16.9	13.6
Length: femur	64.9	71.6	54.4	75.5	68.8	65.6	77.8	58.9
Length: tibia	45.5	45.0	40.1	44.2	41.7	43.1	47.2	37.0
Length: tarsus	67.1	105.6	66.2	81.7	71.9	78.7	78.6	69.1
Length: digit I	242.0	123.0	92.0	191.0	206.0	218.0	212.0	223.0
Length: digit II	136.0	107.0	80.0	117.0	107.0	112.0	117.0	104.0
Length: digit III	85.2	91.3	75.3	64.1	63.6	71.3	79.9	63.5
Phalanx 1: length	34.8	7.7	21.7	25.4	29.0	25.8	23.8	29.5
Phalanx 2: length	16.6	8.2	9.8	15.7	16.6	17.2	18.0	17.9
Phalanx 3: length	14.2	7.7	8.5	13.9	13.4	14.4	14.3	13.2
Phalanx 4: length	16.6	34.7	28.1	21.1	20.5	18.7	21.2	15.9
Phalanx 5: length	17.8	41.6	31.9	23.9	20.5	23.7	22.7	23.9
Phalanx 1: tibia	15.8	3.5	8.9	11.3	12.0	11.1	11.2	10.9
Phalanx 2: tibia	7.5	3.7	4.0	7.0	6.9	7.4	8.5	6.6
Phalanx 3: tibia	6.4	3.5	3.5	6.1	5.6	6.2	6.7	4.9
Phalanx 4: tibia	7.5	15.6	11.5	9.3	8.5	8.0	10.0	5.8
Phalanx 5: tibia	8.1	18.7	13.1	10.6	8.5	10.2	10.7	8.8
Phalanx 2: phalanx 1	47.6	106.8	45.3	61.9	57.3	66.7	75.7	60.6
Phalanx 3: phalanx 1	40.8	100.0	39.3	54.5	46.2	56.0	60.0	44.6
Phalanx 4: phalanx 1	47.5	450.0	130.0	82.8	70.8	72.2	89.2	53.1

tion is carried much further in birds using the foot as a tool for predation; especially is the distal lengthening noticeable. The short basal segments provide the flexibility necessary for grasping perches that are small in diameter and for quick movements of the digits in predation. In the predatory foot the lengthened distal segments constitute a long power-arm that may be quickly flexed on the shorter, basal phalanges.

On the other hand, the cursorily adapted foot possesses abbreviated distal segments. Sometimes the distal segments are lost; *Phoenicopterus* has only 4 phalanges in digit IV. This loss of segments may continue until the entire toe is lost as in the ostrich. Then too, the axes of the digits tend to parallel the longitudinal axis of the body in contrast to the "perching" bird foot in which the median and lateral toes are pulled posteriorly to give better balance and to provide a more efficient grasping organ.

The cathartid foot fits perfectly into neither of these categories. As mentioned previously the foot of *Coragyps* most closely approaches the condition in the chicken which I have used as an example of a familiar running or at least a rapid walking type. The reduced length of all digits and especially digits I and IV in *Vultur* indicates a cursorial adaptation. The feet in *Sarcoramphus* and *Cathartes* appear to be the least cursorily adapted. *Gymnogyps* is intermediate in this respect.

Blechschmidt (1929) has used a ratio (sum of the lengths of the distal phalanges to the sum of the lengths of the proximal phalanges) to obtain a numerical index for use in comparing bird feet. He distinguishes two major foot types—"Baumfuss" and "Lauffuss"—and regards all other "types" as modifications of these two. Disregarding the hallux which reflects other foot modifications, he considered the first two phalanges of digits II and III and the first three phalanges of digit IV as basal segments. Finding that adaptations of structure of digit III did not coincide with the adaptations in the other digits, he emphasized the structure of digits II and IV in determining foot types.

In table 40 I have reduced his fraction indices to decimal indices and have added the values for the cathartids, *Pandion*, *Aquila* and *Gallus*. Phalangeal length in his study was the distance between articulating surfaces. My measurements were made in the same manner.

Indices for digit II reveal a graded series from two typically cursorial types through the cathartids, *Gallus* and *Gyps*, to the owls and hawks. *Coragyps* has the highest ratio of any cathartid, but it is perhaps not greatly higher than in *Vultur* and *Gymnogyps*. *Cathartes* has a ratio that is significantly low. Even though the difference between *Coragyps* and *Gymnogyps* is small, as seen here, it must be held in mind that digit II is longer in *Coragyps*.

In digit III, as indicated by Blechschmidt, we find less indication of the modifications. Except for *Vultur* the cathartids are in a close group near the index for *Gallus*.

Indices for digit IV reveal greater changes. *Gallus* has a relatively high index, with *Vultur* and *Rhea* following. In addition to the fact that within the digit *Vultur* shows greater cursorial adaptations it must be remembered that its fourth toe is shorter than that of any other cathartid.

Therefore, following Blechschmidt in his method of considering only digits II, III and IV, we find that *Coragyps* and *Vultur* are the best adapted cursorially, with *Gymnogyps* intermediate, and *Cathartes* and *Sarcoramphus* the poorest runners or walkers among the New World vultures. These conclusions are identical to those previously determined from study of the digit ratios given in the tables already discussed.

TABLE 40.

Digit II		Digit III		Digit IV	
Ostrich	absent	Ostrich	1.860	Ostrich	5.660
Rhea	1.220	Vultur	1.560	Gallus	1.880
Coragyps	0.666	Accipiter nisus	1.500	Vultur	1.510
Vultur	0.639	Coragyps	1.370	Rhea	1.510
Gymnogyps	0.609	Gymnogyps	1.350	Coragyps	1.440
Gallus	0.562	Gyps	1.330	Gymnogyps	1.360
Serpentarius	0.538	Cathartes	1.320	Sarcoramphus	1.270
Cathartes	0.497	Gallus	1.260	Cathartes	1.240
Sarcoramphus	0.482	Sarcoramphus	1.220	Gyps	1.000
Gyps fulvus	0.333	Rhea	1.220	Serpentarius	1.000
Bubo bubo	0.250	Serpentarius	1.000	Accipiter nisus	0.818
F. tinnunculus	0.250	F. tinnunculus	0.818	Aquila	0.666
Pandion	0.226	Aquila	0.754	F. tinnunculus	0.538
Aquila	0.211	Buteo buteo	0.666	Buteo buteo	0.429
Accipiter nisus	0.176	Bubo bubo	0.538	Pandion	0.305
Buteo buteo	0.176	Pandion	0.500	Bubo bubo	0.250

Muscles of the Hind Limb

M. EXTENSOR ILIO-TIBIALIS LATERALIS

Description.—This muscle forms a thin sheet (fig. 18), the anterior edge of which is more or less intimately connected to M. extensor ilio-tibialis anterior. On its medial surface it is in close contact with and more or less fused to the underlying M. vastus lateralis. Especially is this true in the distal aponeurosis.

Distally the muscle converges in the aponeurosis which covers the external surface of the knee. As may be seen in the drawing, the muscle consists essentially of two functional parts, an anterior and a posterior; the central part of the muscle has only short fibers. Muscle fibers extend farther distally in the more powerful posterior part.

Origin.—By aponeurosis from the most dorsal part of the anterior and posterior iliac crests, extending down over the femoral trochanter (fig. 26). Anteriorly the sheet is in common with the origin of M. extensor ilio-tibialis anterior. Posteriorly the muscle fibers arise from a short aponeurosis near the posterior end of the iliac crest.

Insertion.—The strong posterior part inserts on a line on the outer cnemial crest (fig. 28). The insertion of the anterior portion is partly covered by the origin of the head of the pars interna of M. gastrocnemius from the patellar tendon. Part of the insertion anteriorly is on the inserting tendon of M. ilio-tibialis anterior which, with the insertion of the present muscle, forms a part of the patellar tendon.

Innervation.—A branch of the peroneal nerve emerges between the bellies of M. vastus lateralis and M. extensor ilio-fibularis and enters the posterior part between the

first and second thirds of the belly. The anterior part receives a twig of the femoral nerve which passes ventral to M. iliacus and between M. vastus lateralis and M. extensor ilio-tibialis anterior.

Action.—The major function is extension of the shank; both the cranial and caudal portions aid in this. There is also strong abduction of the limb. Since the major part of the muscle is posterior to the femur there is some tendency to pull the femur posteriorly.

Comparison.—Similar in *Sarcoramphus* and *Coragyps*. In *Cathartes* the origin does not extend as far posteriorly as in *Coragyps*, and the proximal posterior edge of M. extensor ilio-fibularis is not covered. The condition in *Cathartes* is intermediate between that found in other cathartids and that in *Buteo* and *Falco*. In the latter two genera the origin is entirely from the acetabular and preacetabular parts of the ilium (Hudson, 1937:18). In *Gymnogyps* the posterior part is relatively weaker; the two parts are about equally developed, but the fibers in the caudal portion are shorter than in *Coragyps*.

The weakness of the posterior part in *Cathartes* and *Gymnogyps* is important; it lessens the ability to pull the femur posteriorly. Howell (1938, fig. 1) illustrates a well developed, post-acetabular part in *Gallus*. Development of the posterior part is correlated with terrestrial locomotion. Table 41 shows that this muscle is by far the strongest in *Coragyps*, next largest in *Sarcoramphus* and weakest in *Cathartes* and *Gymnogyps*.

M. EXTENSOR ILIO-TIBIALIS ANTERIOR

Description.—A bandlike muscle which forms the anterior edge of the thigh (fig. 18). Distally it is covered by the belly and tendon of M. extensor ilio-tibialis lateralis, with which it is partly fused.

Origin.—Anteriorly the origin is fleshy from the anterodorsal curve of the ilium (fig. 26) but caudally the origin is aponeurotic in common with M. extensor ilio-tibialis lateralis.

Insertion.—Mainly fleshy on the anteromedial surface of the patellar tendon in the middle of its length. Some fibers may extend to the inner corner of the anterior cnemial crest. The head of the pars interna of M. gastrocnemius surrounds the point of insertion and is firmly attached by fascia to M. extensor ilio-tibialis anterior.

Innervation.—A twig of the femoral nerve passes ventral to the midregion of M. iliacus and enters the upper third of M. extensor ilio-tibialis anterior on the inner surface. Two cutaneous branches of the femoral nerve continue externally to emerge between this muscle and M. extensor ilio-tibialis lateralis.

Action.—Simultaneous extension of the shank and flexion of the femur upward and forward.

Comparison.—Little structural variation is found among the New World vultures. In *Cathartes* the insertion is slightly more proximal and is not covered by the pars interna of M. gastrocnemius. Otherwise the muscle is identical in the various cathartids. The muscle is best developed in *Cathartes;* it is somewhat weaker in the other vultures.

M. PIRIFORMIS

Description.—This is a small weak triangular muscle which is easily overlooked since it frequently is closely attached to M. gluteus profundus. The tendon is usually discernible as a separate part of the insertion of M. gluteus profundus (fig. 19).

Origin.—Fleshy from the iliac crest above the antitrochanter, posterior to the origin of M. gluteus profundus and anterior to, but slightly overlapped by, the origin of M. extensor ilio-fibularis (fig. 26).

Insertion.—The tendon inserts on a transverse line on the lateral face of the greater trochanter, posterior and distal to the insertion of M. gluteus profundus. The inserting tendon may be fused with the tendons of Mm. ischiofemoralis and vastus lateralis (fig. 27).

Innervation.—As Howell (1938:77) noted, M. piriformis is innervated by the peroneus nerve which sends a branch anteriorly above the neck of the femur. This branch also serves M. gluteus profundus. In one instance the twig to M. piriformis actually came from within M. gluteus profundus.

Action.—Weak abduction of the femur.

Comparison.—Identical in the genera examined. Volumetric measurement of this muscle is subject to considerable error due to its small size and attachment to M. gluteus profundus. However, the muscle in *Cathartes* is significantly strongest.

M. GLUTEUS PROFUNDUS

Description.—Anteriorly and laterally M. iliacus borders it, and posteriorly M. piriformis overlaps and fuses with it (fig. 19).

Origin.—The origin is fleshy throughout and is from the entire anterior gluteal fossa with the exception of the anterolateral corner where Mm. iliacus and extensor iliotibialis anterior arise. The origin extends posteriorly along the iliac crest to a point above the acetabulum (fig. 26).

Insertion.—All the fibers converge distally to form a crescent-shaped insertion on the lateral face of the femoral trochanter (fig. 27).

Innervation.—Double innervation is present here. The largest nerve entering the muscle is a cranially directed twig from the branch serving M. piriformis; this is a twig of N. peroneus which passes beneath M. piriformis dorsal to Mm. obturator internus and externus. A branch of the femoral nerve emerges between the proximal ends of Mm. iliacus and ilio-trochantericus medius and enters the midventral part of M. gluteus profundus. Thus we are dealing with a bipartite muscle, the posterior part of which has arisen from the deep, postfemoral musculature. Howell (1938:77) does not give a femoral innervation for this muscle in *Gallus*.

Action.—The outer surface of the femur is rotated forward and inward which would tend to bring the lower leg beneath the body.

Comparison.—No differences were noted among the cathartids. Hudson (1937:11) found that this muscle ". . . is subject to no significant modifications." The ratios for relative volume (table 41) indicate that the muscle is strongest in *Gymnogyps* and is weakest in *Coragyps* and *Sarcoramphus*.

M. ILIACUS

Description.—Its anterior edge is much thicker than the posterior due in part at least to the development of M. gluteus profundus which overlies the posterior, proximal part of the muscle. The M. ilio-trochantericus medius borders it caudally and medially and is closely connected to M. iliacus (fig. 19).

Origin.—Fleshy from the ventral edge of the ilium lateral to the origin of M. gluteus profundus and extending caudally to the origin of M. ilio-trochantericus medius (fig. 26).

Insertion.—Partly tendinous on the middle of the lateral face of the femur between the origins of Mm. vastus medialis and vastus lateralis (fig. 27).

Innervation.—The short branch of the femoral nerve that serves M. gluteus profundus sends a twig to the posteroventral surface of M. iliacus in the middle of its length.

Action.—Rotates the outer surface of the femur forward and inward.

Comparison.—The configuration is identical in the genera examined. There is some indication (table 41) that it is sturdiest in *Cathartes* and weakest in *Coragyps*.

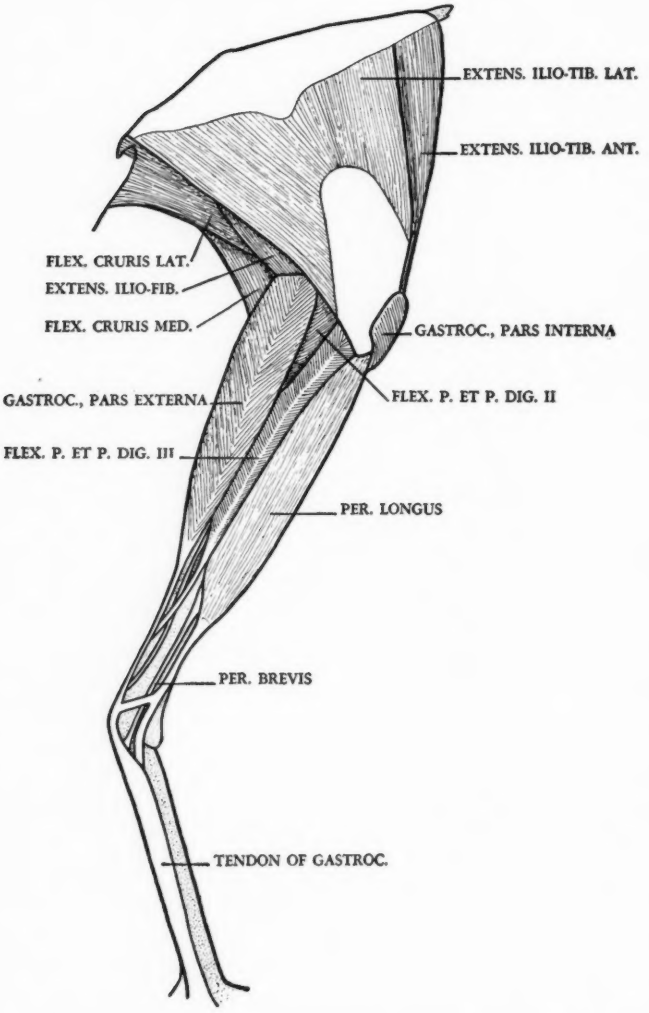


Fig. 18. *Coragyps atratus*. Lateral view of the superficial muscles of the right leg, ×1/2.

M. ILIO-TROCHANTERICUS MEDIUS

Description.—See figure 20.

Origin.—Fleshy from the ventral edge of the ilium between the anterior part of the acetabulum and the posterior edge of the origin of M. iliacus (fig. 26).

Insertion.—Tendinous on a longitudinal line on the lateral face of the femur proximal to the insertion of M. iliacus (fig. 27).

Innervation.—The same branch of the femoral nerve that supplies M. iliacus sends a twig to the anterior edge of the proximal end of the muscle.

Action.—Aids Mm. gluteus profundus and iliacus in rotating the femur forward and inward.

Comparison.—The muscle is largest in *Cathartes;* it is much smaller in the other cathartids. As mentioned previously in discussing M. gluteus profundus and M. iliacus, differences in volumes of the gluteal muscles are small. However, if we consider the total volume of muscles originating on the ilium and inserting on the outer, proximal surface of the femur, important differences may be observed. In *Cathartes* the muscles make up 7.67 per cent of the total leg-muscle volume; in *Coragyps* they are 5.77 per cent, in *Sarcoramphus* 5.56, in *Gymnogyps* 9.23, and in *Vultur* 8.00. This indicates that the power to rotate the femur forward and inward ("toeing in") is greatest in *Gymnogyps* and least in *Coragyps* and *Sarcoramphus.*

M. VASTUS LATERALIS

Description.—On its anteromedial face it is inseparable from M. vastus medialis. The inserting tendons of the two vastus muscles form the bulk of the patellar tendon (fig. 19). In the distal half of its length this muscle covers the femoral attachments of the tendinous loop for M. extensor ilio-fibularis and the accessory heads of M. flexor cruris lateralis. Proximally the belly covers the femoral attachment of M. caudofemoralis.

Origin.—Fleshy throughout (fig. 27). For the most part the origin is from the lateral face of the femur, but in the middle third of the femur it may expand on to the posterior surface. Along its anterior edge this muscle takes origin from the anterolateral face of M. vastus medialis.

Insertion.—After contributing substantially to the patellar tendon, the tendon of M. vastus lateralis continues distally to insert on the entire outer cnemial crest proximal to the origin of M. peroneus longus (fig. 28).

Innervation.—The branch of the femoral nerve serving M. iliacus also sends a twig laterodistally across the proximal anterior face of M. vastus medialis (fig. 19). As it disappears between the proximal parts of the two vastus muscles it sends a branch to each muscle.

Action.—Powerful extension of the shank.

Comparison.—The only variation noted is in *Gymnogyps* and *Vultur;* the origin does not extend on to the posterior surface of the femur in these forms.

M. VASTUS MEDIALIS

Description.—It is bordered and partly covered laterally and anteriorly by M. vastus lateralis, to which it is fused. The inserting tendon of M. iliacus separates this muscle proximally from M. vastus lateralis (fig. 19).

Origin.—For the most part the origin is fleshy on the anterior face of the femur from the region between the head and the trochanteric ridge distally to the rotular groove. In its middle half the origin extends on to the anterior half of the medial surface of the femur (fig. 27).

Insertion.—In common with M. vastus lateralis, but it also includes the anterior and inner cnemial crests (fig. 28). The common inserting tendon of these muscles is pierced by the tendon of M. ambiens in its passage laterally and distally across the knee. The tendon of M. ambiens is superficial to the patella and proceeds laterally beneath the knee tendon.

Innervation.—As described for M. vastus lateralis. There is extensive arborization of the nerve to M. vastus medialis; as many as five to seven twigs are distributed along its length. On its medial face the muscle receives one or two twigs from another branch of the femoral nerve.

Action.—Powerful extension of the shank.

Comparison.—Small differences in the volume of the muscle (table 41) are the only variations. Total volume of the four shank extensors (vastus and ilio-tibialis muscles) makes up the greatest per cent of the total leg-muscle volume in *Coragyps* (22.15 per cent). In the other cathartids the percentages are: *Cathartes*, 16.33; *Sarcoramphus*, 16.69; *Gymnogyps*, 18.3; and *Vultur*, 18.0. The greater volume in *Coragyps* is due to large extensor ilio-tibialis muscles. One would expect an increase in these uncrowded, superficial muscles in any muscular adaptation for better extension of the lower limb. Only in *Gymnogyps* are the deep extensors larger. The most change has evidently occurred in M. ilio-tibialis lateralis. The M. ilio-tibialis anterior of this group also functions to pull the femur forward; its inclusion here, however, does not materially change the relative total volumes given above, since it shows little variation in volume among the genera.

M. EXTENSOR ILIO-FIBULARIS

Description.—In the third quarter of the femoral length a strong round tendon is formed which passes through a tendinous loop arising partly from the femur and partly from the tibia (Hudson, 1937, fig. 3, p. 85). The peroneus nerve and blood vessels accompany the tendon through the loop. The tendon goes between the pars externa and pars media of M. gastrocnemius to its insertion on the shank. Deep to M. gastrocnemius it passes external to M. flexor hallucis longus and M. flexor digitorum longus and medial to the origin of M. flexor perforatus digiti II (figs. 18 and 19).

Origin.—Fleshy from a wide and deep line on the iliac crest posterior to the antitrochanter (fig. 26).

Insertion.—Tendinous on the tubercle of the fibula, which lies near the center of the fibular crest of the tibia.

Innervation.—Howell (1938:74-75) gives the innervation of this muscle as the peroneal nerve. In the cathartids it was impossible to determine whether the branch came from the peroneal or tibial nerves since the nerve trunks are together for most of the length of the femur and are not distinctly separated for their entire length external to the pelvis, as he has figured them in *Gallus*. However, M. extensor ilio-fibularis also receives two short crural flexor branches of N. tibialis. These come from the trunk serving M. flexor cruris lateralis.

Action.—Strong flexor of the shank. There may be some tendency to rotate the shank to make the bird "toe out" when the lower leg is flexed upon the femur.

Comparison.—In *Cathartes* and *Gymnogyps* the origin extends farther forward; it covers the antitrochanter and is tendinous over the posterior one-third of the origin of M. piriformis. In the former this muscle is not so completely covered by M. ilio-tibialis lateralis because of the more anterior placement of this latter muscle. This muscle is similarly developed in these vultures, but it may be somewhat weaker in *Coragyps*.

M. FLEXOR CRURIS LATERALIS

Description.—Because of the large size of M. extensor ilio-fibularis, which is superficial to the anterior part of the muscle, this part is somewhat concave in its upper two-thirds. The muscle is superficial to M. flexor cruris medialis but is separated from it by crural flexor branches of N. tibialis and M. caudofemoralis (figs. 18-20).

The accessory part of the muscle is in two fairly distinct parts—the usual, large dorsal belly of about the same width as the main belly and a more distal and medial part which parallels the pars media of M. gastrocnemius (fig. 20). This latter part is in all probability a part of the true shank musculature. Gadow (1891:163) considered the accessory head in *Larus* as a direct continuation of the pars media of M. gastrocnemius. This would appear to be true in the cathartids.

Origin. Main head.—Tendinous from the posterior tip of the pubis and from fascia lateral to the cloaca and fleshily from the posterior tip of the iliac crest and from the

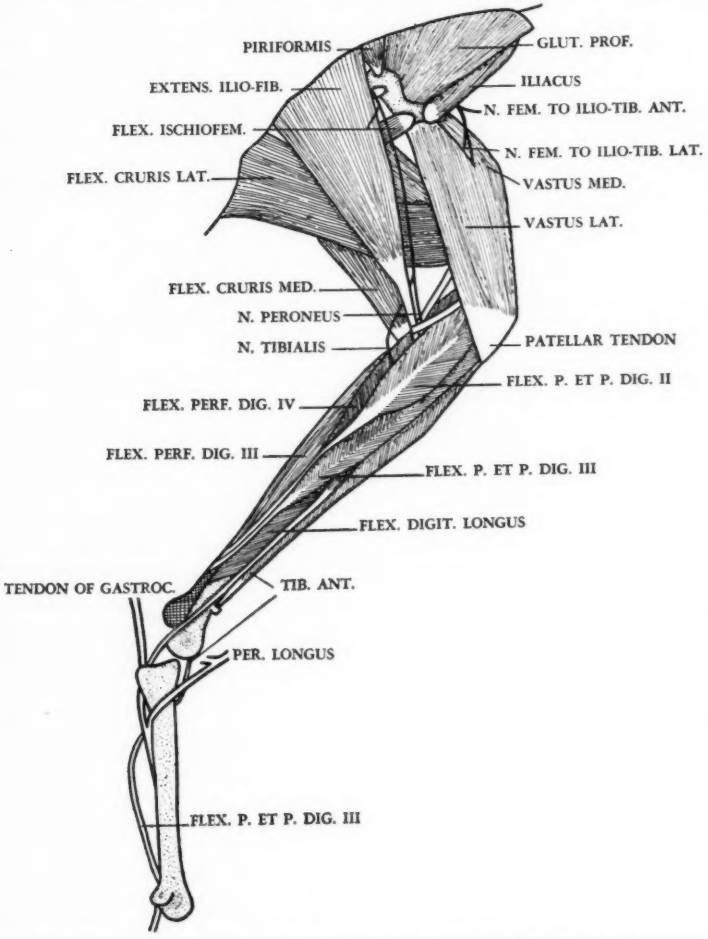


Fig. 19. *Coragyps atratus*. Lateral view of the right leg showing a second layer of muscles, ×1/2.

caudal tip of the ischium (fig. 26). I can not find, as Hudson (1937:22) states, that the fascial origin of this muscle extends to the caudal vertebrae any more than do the origins of other postfemoral muscles. It is true that fascia covers the dorsal aspect of the ilium, but the only true fascial origin is as noted above.

Proximal accessory head.—The origin of this part acts as one point of insertion of the main head and is usually considered as such. This head arises fleshily from a triangular area on the posterolateral aspect of the femur (fig. 27).

Distal accessory head.—Fleshy from the inner posterior surface of the femur proximal to the popliteal area and by fascia from M. adductor profundus near its insertion. The point of origin is distinct from that of the other accessory head although the bellies may be intimately connected farther distally.

Insertion. Main and proximal accessory heads.—As noted above the main head may use the origin of this accessory head as the insertion. However, the two heads insert by means of a common tendon on the pars media of M. gastrocnemius and on the tendon of M. flexor cruris medialis.

Distal accessory head.—Inserts tendinously on the tendon of the two other heads, but the main insertion is farther distally on the posterior surface of the pars media of M. gastrocnemius.

Innervation.—The main head is served by short crural flexor branches of N. tibialis which pass external to M. flexor ischio-femoralis and internal to M. caudofemoralis and enter the medial surface. Cutaneous branches of these flexor nerves run across the external faces of M. flexor ischiofemoralis and M. caudofemoralis and the anterior edge of the muscle under consideration. The proximal accessory head receives a twig from the main trunk of N. tibialis, and the distal head is innervated by still another twig from the same nerve.

Action.—Contraction of the main head would first cause retraction and flexion of the shank and extension of the tarsus. Greater contraction would pull the femur posteriorly. The accessory heads flex the shank and extend the tarsus due to their insertion on the tendon of M. gastrocnemius.

Comparison.—In *Cathartes* the origin is compressed from front to back and is from the ischium for the most part; it does not extend caudally to the tip of the pubis and arises from this bone only in the region below the tip of the ischium. The distal accessory head has a larger and more distal point of origin.

The entire main head of the muscle is posterior to M. extensor ilio-fibularis in *Gymnogyps*. It is a thick bandlike muscle of uniform width. Origin of the proximal accessory head is much more limited than in *Coragyps* (fig. 27).

In *Vultur* and *Sarcoramphus* the origin of the main head does not extend dorsally to the iliac crest, but it occupies all of the ischium posterior to the origin of M. flexor ischio-femoralis and the entire lateral surface of the pubis caudal to the adductor muscles. It may extend on to the abdominal musculature between the free tips of the pubis bones. The femoral origin of the accessory heads is large. It occupies the area shown in figure 27 and also extends distally along the median edge of the popliteal area to the internal condyle where it is medial to the origins of the toe flexors. The distal accessory head inserts fleshily on the tendon of M. gastrocnemius between the internal and medial heads, and its origin is in part from the tendinous insertion of M. adductor profundus.

Table 41 indicates that M. flexor cruris lateralis is approximately equally developed in the cathartid genera with the exception of *Gymnogyps* in which it is decidedly weaker. The smallness of the muscle in the latter genus combined with poorer femoral attachments shows that the efficacy of this muscle is least in the California condor. The more posterior origin of the main head and the large areas of fleshy attachment in *Vultur* and *Sarcoramphus* make this muscle more effective than that in the other vultures. Although the muscle is about the same size in *Coragyps* and *Cathartes* it is more efficient in the former because the main head is more caudal in origin and thus its vector

of effectual force is greater. Consequently, the series in order of decreasing power of this muscle is *Vultur*, *Sarcoramphus*, *Coragyps*, *Cathartes* and *Gymnogyps*. The difference is greatest between the last two.

M. FLEXOR CRURIS MEDIALIS

Description.—Opposite the distal end of the femur it forms a wide thin tendon which enters the shank musculature between the pars interna and the pars media of M. gastrocnemius. As the tendon parallels that of M. flexor cruris lateralis they are strongly attached. There may also be considerable fascial connection to the fleshy parts of the accessory heads of M. flexor cruris lateralis (fig. 20).

Origin.—Fleshy from the ischium immediately ventral to the origin of M. flexor ischio-femoralis and slanting posteroventrally across the pubis and on to the abdominal wall (fig. 26). The origin becomes tendinous in its posterior one-third, due in part at least to the development of the overlying M. flexor cruris lateralis.

Insertion.—By a wide, thin tendon on the medial surface of the tibia 2 cm. distal to the cnemial crest and immediately distal to the origin of M. plantaris. It also inserts on the tendon of insertion of M. flexor cruris lateralis.

Innervation.—The nerve supply apparently may be from two sources. Short crural branches of N. tibialis pass beneath M. caudofemoralis and enter the proximal external part of the muscle. Two small obturator twigs emerge ventral to the pubis and go to the proximal medial surface. Howell (1938:77) did not find any obturator innervation of this muscle in *Gallus*, but in five out of eight cathartid specimens such nerves were observed. They did not pass through the muscle. However, in one instance very high crural branches of N. tibialis entered the muscle in the same manner.

Action.—Strong flexion of the shank accompanied by some adduction of the limb. The attachment to the tendon of M. flexor cruris lateralis causes this muscle to aid in the flexion of the shank and extension of the tarsus through the medium of the tendon of M. gastrocnemius.

Comparison.—In *Cathartes* the insertion is more proximal. In *Vultur* the origin is mixed fleshy and tendinous from a narrow line, and there is little or no connection to the M. flexor cruris lateralis or its tendons. Only weak attachment to this muscle is present in *Gymnogyps*.

In *Sarcoramphus* the origin is entirely fleshy, and there is no connection to either adductor muscle. At the caudal end of the origin there is thin tendinous origin from the abdominal musculature.

Table 41 shows the relative development of this muscle. The larger size in *Cathartes* is largely offset by the more proximal insertion. Absence of effective attachment to M. flexor cruris lateralis, as in *Vultur* and *Gymnogyps*, precludes any extension of the tarsus.

M. CAUDOFEMORALIS

Description.—M. caudofemoralis is a small thin elongated muscle passing from the tail to the thigh. It enters the thigh ventral to the caudal tip of the iliac crest and runs diagonally across the origin of M. flexor ischiofemoralis and across the upper end of the adductor muscles. M. flexor cruris lateralis is immediately superficial to it, as are N. tibialis, N. peroneus and the postfemoral blood vessels. Although it is quite variable in its development within a species, in *Coragyps* it becomes fleshy only after emerging ventral to the tip of the ilium; in its distal third near the femur it again becomes tendinous (fig. 20).

Origin.—Tendinous; a small thin tendon runs over the ventral surface of the infracoccygis to insert on the most ventral tip of the pygostyle ventral to part of the insertion of M. levator coccygis (fig. 20). Although this is the origin of the muscle as shown by its development and source of innervation, functionally it is the insertion.

Insertion.—Tendinous on a small spot on the postero-lateral corner of the femoral

shaft 33 millimeters from its proximal end, or just above the middle of its length (fig. 27).

Innervation.—From a crural branch of N. tibialis in the anterior third of its fleshy belly.

Action.—Two functions are possible. The tail may be depressed and drawn laterally, and the femur may be pulled posteriorly. In forms such as geese which possess both the pars iliofemoralis and pars caudifemoralis the muscle may be a strong flexor of the thigh; in gulls, owls and hawks which have only the pars caudofemoralis (Hudson, 1937:22) it is a weaker flexor of the femur. In *Cathartes* and *Coragyps* the weak tendinous condition of the pars caudofemoralis and the absence of the pars iliofemoralis make the action of the muscle effective chiefly on the tail. The habit some birds have of moving the tail to one side as the leg on that side is moved forward may in part be the result of the tendinous action of this muscle. There may be some value in this shifting of the tail. As the femur is moved forward to its maximum extent, the distal end of the muscle is pulled anteriorly with it; this pulls the tail laterally. The shifting of the tail aids in moving the center of gravity toward the side on which the foot is on the ground. Meanwhile the opposite foot is lifted from the ground, and as it moves forward the tail moves toward the side, shifting the body weight to a certain extent and thus aiding in the balancing of the body on the foot resting on the ground.

Comparison.—In *Cathartes* the muscle is stronger but inserts more proximally on the femur; it is fleshy almost up to the point of attachment on the femur. The muscle is absent in *Gymnogyps*, *Sarcoramphus* and *Vultur*! Garrod (1873:626) states that the accessory part, i.e., the pars iliofemoralis, is absent in the Cathartidae and that the pars caudifemoralis is small in *Coragyps atratus*. He found neither part of M. caudofemoralis in *Gyparchus* [*Sarcoramphus*] *papa*.

Garrod (1874) used the two parts of M. caudofemoralis in his myological formulae. Hudson (1937:60) records the pars caudofemoralis as absent only in *Colymbus;* he thinks it ". . . should never have been used in a myological formula, since it is present in almost all birds, being absent mainly in certain aberrant genera and species." Pars iliofemoralis is absent in many forms.

Howell (1938:77) discusses the M. caudofemoralis, its origin and homology. It is a muscle of the ventral division and has a close relationship to the pubo-ischiotibial layer of amphibians and reptiles. It is unlikely that twice in the history of the New World vultures this muscle would have developed. Therefore, it is of value in determining the phylogeny of this group, indicating that *Coragyps* and *Cathartes* are the more primitive. Loss of the muscle might more likely have occurred independently in three genera. Thus this muscle offers no definite evidence on the relationship between *Gymnogyps*, *Sarcoramphus* and *Vultur* which lack it.

M. FLEXOR ISCHIOFEMORALIS

Description.—See figure 20.

Origin.—The origin is fleshy from the lateral face of the ilium posterior to the ilio-ischiatic fenestra (fig. 26).

Insertion.—Tendinous on a longitudinal line on the external face of the greater trochanter of the femur posterior to the insertion of M. iliacus and distal to the insertions of Mm. gluteus profundus and piriformis (fig. 27).

Innervation.—A short flexor branch of N. tibialis enters the middle of the dorsal edge of the belly.

Action.—It is a strong rotator of the femur causing the bird to toe out, and moving the femur backward and inward. The lever arm is too short for much effective backward pull of the femur.

Comparison.—The attachments are identical in the forms dissected. The M. flexor ischiofemoralis is best developed in *Cathartes*, and is only slightly weaker in *Gymnogyps*.

The muscle is least developed in *Vultur;* in *Coragyps* it is smaller than in *Gymnogyps* (table 41). Size of the muscle is not correlated with size of the bird. It may be related to running ability, but more probably the large size in *Cathartes* and *Gymnogyps* is to be correlated with their habit of standing pigeon-toed when relaxed. Tracks made by *Cathartes* when walking or running do not show this toeing in. The only muscles capable of turning the toes out are the obturators, the M. caudofemoralis and the muscle being considered. The obturators are equally developed in cathartids and the M. caudofemoralis is too weak for effective action on the leg. Thus, the M. flexor ischiofemoralis is the significant muscle in the elimination of the pigeon-toed stance. The larger size in the turkey vulture and the California condor may be a modification to aid in this elimination.

M. ADDUCTOR SUPERFICIALIS

Description.—See figure 23.

Origin.—The origin is tendinous in its anterior fifth and is a thin line on the ventral border of the ischium in the anterior half of this bone (fig. 26).

Insertion.—Fleshy on the medial part of the posterior face of the femur along the distal three-fifths of its length, extending distally to the proximal edge of the popliteal

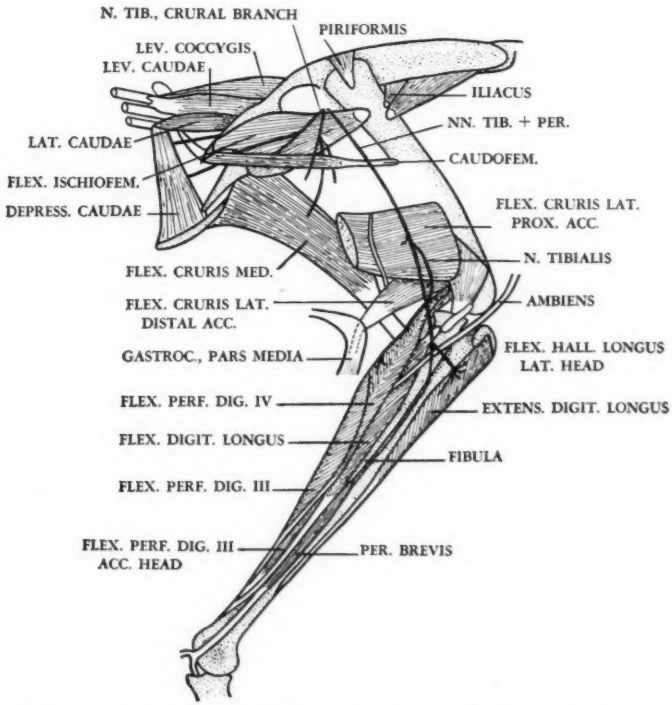


Fig. 20. *Coragyps atratus.* Lateral view of the tail and the right leg showing a third layer of muscles, ×1/2.

area (fig. 23). The inner edge of the insertion is marked by the sharp ridge on the posteromedial angle of the lower femur.

Innervation.—An anterior branch of N. obturator enters the deep side of the muscle between the first and second thirds.

Action.—Pulls the femur posteriorly. See discussion of function of M. adductor profundus.

Comparison.—In *Cathartes* the muscle entirely covers M. adductor profundus; the latter is not visible in external view. The anterior part of this muscle is much thicker than the posterior part. It is possible, but very difficult, to separate the thin posterior portion from the underlying M. adductor profundus. The *posterior* one-fifth of the origin is tendinous, and the distal posterior part of the insertion is tendinous and inseparable from the tendon of M. adductor profundus.

In *Gymnogyps* M. adductor profundus is visible as a strip one-fourth inch wide along the posterior edge of this muscle. The proximal anterior part of the origin and the belly are excavated to accommodate the large belly and origin of M. flexor ischiofemoralis. The anterior one-half of the origin is tendinous; the distal part of the insertion is very thin and tendinous, probably to allow for the heads of the flexor muscles that originate from the inner popliteal area of the femur.

The origin which extends farther posteriorly in *Vultur* is almost entirely tendinous, and the insertion is entirely fleshy; the distal part of the insertion is in common with M. adductor profundus. In *Vultur* and *Sarcoramphus* M. adductor profundus is covered by M. adductor superficialis, and the two are inseparably fused along their posterior borders. The origin is fleshy throughout but is underlaid by a strong aponeurosis anteriorly in *Sarcoramphus*.

M. ADDUCTOR PROFUNDUS

Description.—Proximally it is divided into two parts, a thick spindle shaped posterior part and a wide, thin anterior part which is separated from M. adductor superficialis proximally by branches of N. obturator (fig. 22). The anterior part parallels the origin, insertion and direction of fibers of M. adductor superficialis, but is completely separated from it. Both parts of M. adductor profundus are completely fused distally (fig. 22).

Origin. Anterior Part.—From the ischium posterior to the obturator foramen and ventral to the origin of M. adductor superficialis (fig. 26). It is fleshy in its anterior two-thirds, but posteriorly beneath the edge of the posterior part it is tendinous. This is probably the result of the size of the overlying M. adductor superficialis.

Posterior Part.—Fleshy from spot in middle of the length of the ischium and continuing ventrocaudally across the pubis (fig. 26) and on to the abdominal muscles. Origin ventral to the pubis is tendinous.

Insertion.—The inserting ends of the two parts are fused for the distal half of the length of the belly (fig. 26). The insertion continues distally on the medial surface of the femur to the inner side of the internal femoral condyle where it is limited medially by the origin of M. femoritibialis internus. The insertion is covered medially by the bellies of the Mm. femoritibialis internus and ambiens.

Innervation.—A branch of N. obturator crosses the anterior part obliquely and sends twigs to this part. As it passes distally and disappears between the anterior and posterior parts of the muscle just proximal to their fusion the nerve arborizes and sends twigs to the medial surface of the posterior part.

Action.—Aids M. adductor superficialis in pulling the femur posteriorly. Its deep position in the thigh may cause some femoral adduction. An important function which this muscle shares with Mm. adductor superficialis, flexor cruris lateralis, flexor cruris medialis and extensor ilio-fibularis is that of maintenance of body position. Muscles extending from the pelvis to the posterior surface of the leg may move the leg posteriorly or may move the postacetabular part of the pelvis ventrally if the foot and leg are planted firmly on the ground. In the latter instance the ventral movement raises the forepart of the trunk, using the head of the femur as a fulcrum. Thus these muscles are

important in maintaining an upright body position. Still another function is performed by this upward tilting of the anterior part of the body. In feeding, these New World vultures often seize the carcass with the bill and tear off chunks of flesh by pulling back with feet firmly set on the ground. The postfemoral muscles listed above aid the muscles of the neck and back in this task.

Comparison.—In *Cathartes* there is no separation into anterior and posterior parts, but the parts are indicated by greater thickness in the anterior area which arises by fleshy fibers and by the fact that the posterior two-thirds of the origin is tendinous. Only a partial separation proximally into two divisions is found in *Gymnogyps*. The posterior one-third of the origin is tendinous; it does not extend on to the abdominal musculature. The muscle is uniformly thin.

In *Vultur* the undivided muscle is of uniform thickness. The origin is mixed fleshy and tendinous, and the insertion is tendinous except in its distal one-fifth, medial to the popliteal area. In the condor this muscle has two outstanding features—it is fused along its posterior edge to the overlying M. adductor superficialis, and it is entirely covered medially by a thick, stringy aponeurosis. Some muscle fibers arise from this aponeurosis, but the important fact is that this sheet acts as a support for the femur without the necessity of muscle activity. The strong fibers of the sheet limit the distance to which the distal end of the femur can swing forward. At the most forward point the femur is held with little or no effort. This may be an adaptation to carry the greater weight of this bird. At the same time it fixes the end of the femur to provide a more stable base for action of the lower leg in springing or running.

In *Sarcoramphus* the origin of the posterior part is entirely tendinous and is limited to the ventrolateral corner of the pubis, except for some extension posteroventrally on to the abdominal musculature.

The main function of the adductors is the same—flexion of the femur and/or maintenance of body position; but as mentioned previously the profundus part may adduct the femur. Considering the whole adductor mass (table 41) we find that the muscles are relatively strongest in *Gymnogyps*. In the other genera the muscle mass is about equally developed. In *Vultur* the adductors are more effective than the volumes indicate due to the more posterior origin and the aponeurosis; thus the two large condors possess the most effective adductor mass. Therefore, there probably is a correlation with the weight of the bird. Although the mass is approximately the same in the three smaller forms, it is interesting that the M. adductor superficialis is more than twice the size of the M. adductor profundus in *Cathartes*. The two muscles are equally developed in *Coragyps*.

M. AMBIENS

Description.—A small, thin bandlike muscle lying superficially on the medial surface of the thigh just anterior to M. femoritibialis internus is M. ambiens. The belly extends down to the region just above the internal femoral condyle where it gradually decreases in width to form a thin, flat tendon that passes along the anterior edge of M. femoritibialis and goes obliquely distally and laterally through the patellar tendon. On the anterolateral surface of the caput tibiae it either perforates the head of M. flexor perforans et perforatus digiti III or separates the two parts of the head as the case may be and crosses the external face of the fibula above and deep to the insertion of M. extensor ilio-fibularis.

Origin.—By a wide and thin, but relatively short tendon from the pectineal process of the ilium.

Insertion.—As Hudson (1937:15) points out M. flexor perforatus digiti II is a direct continuation of this muscle. However, it also forms a part of the origins of Mm. flexor perforatus digiti III and IV.

Innervation.—Howell (1938:74-75) states that M. ambiens is served by the femoral nerve. In two of my specimens it seemed that there was also some obturator innervation. Gadow (1891:145), however, gives the innervation as from the last anterior nerve branch of the middle part of the crural plexus together with the M. femoritibialis internus and a part of M. femoritibialis medius.

Action.—Aids in flexing digits II, III and IV, but the major effect is on the second toe. Adduction of the leg is possible, but such action would be weak.

Comparison.—The only variation is in the manner of insertion. In *Cathartes* there is little or no connection between the tendon of M. ambiens and M. flexor perforatus digiti II; the tendon of M. ambiens passes to the accessory head of M. flexor perforatus digiti III. The insertion is the same in *Gymnogyps* and *Coragyps*, and in *Vultur*, *Sarcoramphus* and *Cathartes*. There is no significant difference here, however, since it is merely a matter of degree of connection between tendons, which is variable between individuals.

M. ambiens is equally developed in *Cathartes* and *Gymnogyps*, and in *Sarcoramphus*, *Coragyps* and *Vultur;* it is much larger in the latter two. Gadow (1891:146) has tried to correlate the presence of M. ambiens with the type of ground locomotion, but he could not decide whether the configuration of M. ambiens was cause or result. He cites so many exceptions to all his attempts at correlation that one is led to believe there is no positive relation between the presence of M. ambiens and the ability to run, walk, swim or grasp with the feet.

M. FEMORITIBIALIS INTERNUS

Description.—This bipennate muscle lies on the posteromedial angle of the femur along the distal two-thirds to three-fourths of this bone (fig. 23). It increases in size distally as far as the level of the internal femoral condyle. At this point it converges abruptly to form a short, thin tendon that passes along the medial surface of the patellar cap beneath the tendon of M. ambiens. The belly may extend somewhat below the level of the internal condyle.

Origin.—Fleshy from the inner surface of the second and third fourths of the femoral shaft (fig. 27).

Insertion.—Tendinous on the middle two centimeters of the inner cnemial crest of the tibia (fig. 28). There is also much fascial attachment to the patellar tendon and to the origin of the pars interna of M. gastrocnemius.

Innervation.—A twig from the branch of the femoral nerve to M. ambiens enters the anterior edge of this muscle in the upper half of its length.

Action.—Aids Mm. vastus lateralis and medius in extending the shank. Its chief function appears to be counterclockwise rotation, as viewed from the foot, and adduction of the lower limb. This is perhaps useful in the elimination of a straddling walk.

Comparison.—In *Cathartes* and *Gymnogyps* the muscle is as described for *Coragyps*. The origin in *Sarcoramphus* and *Vultur* extends farther proximally, and an accessory head is present in the latter. This arises from a thin line on the shaft posterior to the origin of the main head; the small belly lies posterior to the tendon of the main head and ends distally at the tip of the internal condyle where it attaches to the main tendon.

The muscle is best developed in *Coragyps;* it is equally developed in the other genera.

M. PSOAS

Description.—A small weak muscle lying on the medial side of the thigh but deep to M. ambiens. The belly is short and narrow. Anteriorly the muscle is bordered by femoral nerves and blood vessels.

Origin.—Fleshy from the ventral border of the ilium just anterior to the acetabulum and ventral to the origin of M. ilio-trochantericus medius (fig. 26).

Insertion.—Fleshy on a small, round area on the posteromedial surface of the femur immediately proximal to the origin of M. femoritibialis internus.

Innervation.—A small branch of the femoral nerve enters the anterior edge of the muscle.

Action.—Any action by this muscle is weak, but it tends to rotate the posterior surface of the femur forward and outward, adducting it at the same time.

Comparison.—Identical in the various cathartids.

M. OBTURATOR EXTERNUS

Description.—Externally the muscle is composed of two distinct parts—one above the inserting tendon of M. obturator internus, the other ventral to the tendon; the lower part is larger (fig. 23). At the point of insertion the two parts form a common tendon superficial to the tendon of M. obturator internus. Beneath this tendon the two parts fuse and insert on it throughout its exposed length.

Origin. Upper part.—Fleshy from an elongated but narrow line on the ischium immediately posterior and ventral to the antitrochanter and dorsal to the obturator foramen but extending medially on to the dorsal edge of the foramen. It also extends ventrally on to the connective tissue covering the anterior part of the foramen; it is in this region that the origins of the two parts coalesce.

Lower part.—Fleshy from the pubis at the anteroventral corner of the obturator foramen and extending dorsally to fuse with the fibers of the upper part (fig. 23).

Insertion.—Mixed fleshy and tendinous on the obturator ridge of the femoral trochanter (fig. 27). The superficial portion is tendinous and lateral to the tendon of M. obturator internus. The deeper part, the chief insertion, is fleshy and deep to the tendon of the internal obturator muscle.

Innervation.—Twigs from the obturator nerve enter the deep edge of the muscle mass.

Action.—Works with Mm. obturator internus, flexor ischiofemoralis and caudofemoralis to rotate the lateral face of the femur backward and inward. However, the extensive fleshy insertion on the posterior surface of the trochanter increases the effectiveness of the muscle in pulling the femur posteriorly without so much rotation.

Comparison.—Similar in the Cathartidae. In the two large condors the distal two-thirds of the M. obturator internus tendon external to the pelvis are completely surrounded by the fleshy elements of M. obturator externus, and some of the fibers of this later muscle originate from the tendon.

It was impossible to remove all of this muscle for volumetric study. No major differences in development were noted.

M. OBTURATOR INTERNUS

Description.—M. obturator internus is a flat, pennate muscle all of which, except the tendon of insertion, lies within the pelvis. No fleshy fibers extend out of the obturator foramen. It is triangular in shape, but is very broad posteriorly and is attenuated anteriorly. The fibers converge on the single central tendon which is not bifurcated.

Origin.—Fleshy from a large area on the medial side of the ischium extending dorsally from the ligamentous attachment between the pubis and ischium to the ilium and posteriorly from the obturator foramen to the angle of the ilium and ischium. Ventrally it extends farther caudally on the ischium. There is no origin from the pubis.

Insertion.—By a strong tendon emerging from the obturator foramen and extending across the lateral face of M. obturator externus to insert on the trochanter of the femur in the middle of the insertion of M. obturator externus but more or less superficial to it. The tendon is encased, except on its lateral surface by M. obturator externus.

Innervation.—Tibial nerve and often an obturator nerve inside the pelvis.

Action.—Rotates the lateral face of the femur backward and inward, a powerful action due to the relatively strong muscle and its lateral insertion on the femoral trochanter.

Comparison.—In *Cathartes* and *Sarcoramphus* the muscle fibers extend outside the pelvis along the proximal one-half of the ventral edge of the exposed tendon. In *Sarcoramphus* and the two large condors the belly has two separate tendons within it. These fuse to form the inserting tendon at the anterior end of the belly. The larger dorsal tendon extends posteriorly into the belly for two-thirds the length of the belly; the smaller ventral tendon is approximately one-half as long as the belly.

Volumetric study indicates that the muscle is equally developed in the several genera (table 41).

M. GASTROCNEMIUS

Description.—The gastrocnemius muscle complex, composed of three muscles, is the superficial mass of the median, posterior and posterolateral surfaces of the upper shank. After fusion of the tendons from the three heads is accomplished about two-thirds of the way down the tibia, the common tendon is the largest and most superficial of the tendons passing over this joint and is the major contributor to the tibial cartilage which surrounds the posterior face of the joint.

PARS INTERNA

Description.—This thin elongated triangular belly covers the proximal two-thirds of the anteromedial side of the shank (fig. 18). A tendon which is formed two-thirds of the way down the shank is continuous posteriorly with the tendon of the pars externa.

Origin.—The origin is chiefly fleshy from the median side of the caput tibiae and from the inner third of the patellar tendon. It extends anteriorly to lap over on to the lateral face of the inner cnemial crest.

Innervation.—The tibialis nerve along with blood vessels comes from the posterior face of the tibia just distal to the insertion of M. flexor cruris medialis. It enters the middle of the deep surface of the pars interna. This branch of the tibialis nerve comes from a main tibialis trunk which courses distally on the shank, internal to M. plantaris.

Comparison.—In *Cathartes* the tendon is formed three-fourths of the way down the shank. There may also be a small tibial nerve twig that enters the muscle above the insertion of the M. flexor cruris medialis. In *Gymnogyps* the pars interna is smaller and bandlike. The belly extends down almost to the tibial cartilage before gradually forming a tendon. In *Vultur* the origin is entirely fleshy. One-fourth of the way down the shank this belly fuses with the pars media, and both give rise to a tendon only halfway down the tibia. In the second fourth of the tibial length in *Vultur*, the common tendon of the pars interna and pars media is joined by the inserting tendon of the second accessory head of M. flexor cruris lateralis.

PARS EXTERNA

Description.—This part of the gastrocnemius forms the posterior and posterolateral sides of the upper shank (fig. 18). At the level of the external femoral condyle the tendon of origin widens into a thick belly which extends farther distally than the belly of the pars interna. Approximately in the middle third of the tibia the bellies of the pars interna and pars externa are firmly attached to each other, but complete fusion of the tendons does not occur before the last third of the tibial length is reached.

Origin.—Part of the origin is fleshy from the fascia of the knee, but the main origin is by a small flat tendon from the flexor attachment area on the outer surface of the external femoral condyle (fig. 27). This tendon is inseparable from the outer femoral part of the loop for M. extensor ilio-fibularis; there often is fleshy origin from the ilio-fibularis loop.

Innervation.—From the branch of the tibialis nerve which enters the shank musculature medial and distal to the inserting tendon of M. extensor ilio-fibularis.

Comparison.—In *Cathartes* the belly of the pars externa does not extend as far distally as the belly of the pars interna, and complete fusion of the tendons occurs only in the distal fifth of the shank length. In *Vultur* the pars externa fuses with the pars interna one-fourth to one-third of the way down the tibia, and the belly of the pars externa is confined to the upper half of the tibial length. No differences between *Gymnogyps*, *Sarcoramphus* and *Coragyps* were observed.

PARS MEDIA

Description.—This, the smallest of the heads of M. gastrocnemius, is covered laterally by the pars externa but separated from it by the tendon of M. extensor ilio-fibularis, its tendinous loop, the peroneus nerve and one main trunk of the tibial nerve. Medially

it is separated from the pars interna by the insertion of M. flexor cruris medialis and the other main trunk of the tibial nerve. In the distal part of the length of the posterior surface of the pars media is inserted the tendon dividing M. flexor cruris lateralis and its dorsal accessory head (fig. 20). The fibers of the pars media are one-third the length of those of the pars interna and one-half the length of those of the pars externa.

Origin.—Tendinous from a spot on the posteromedial surface of the femur. The belly is formed abruptly where the tendon of origin passes between the two main trunks of the tibialis nerve.

Innervation.—By the same branch of the tibialis nerve that serves the pars externa.

Comparison.—In *Cathartes* and *Gymnogyps* the tendon of the second or ventral accessory head of M. flexor cruris lateralis overlies the distal part of the pars media but is not inserted on it. The accessory head inserts on the gastrocnemius tendon at the point of fusion of the tendons of the pars interna and the pars externa. In *Cathartes* the pars media appears to have no inserting tendon; the distal ends of the muscle fibers attach to the undersurface of the pars externus. In *Vultur* I could find no attachment of M. flexor cruris lateralis or its accessory heads to M. gastrocnemius.

Insertion.—The tendon of M. plantaris is closely adherent to the common tendon of M. gastrocnemius in the lower shank region. After passing over the tarsal joint the tendon fans out to cover the posterior surface of the tarsus and to ensheath all the post-tarsal tendons. There is some fibrocartilaginous insertion on the lateral calcaneal ridges of the hypotarsus, but the main insertion is on the ridge on either side of the posterior tarsal groove and on strong fascia surrounding the posterior half of the distal part of the tarsus; the fascia covers the entire sole of the foot and may even extend on to the basal phalanges of digits II, III and IV.

The insertion in *Cathartes* and *Sarcoramphus* is the same as described for *Coragyps*. In *Gymnogyps* the insertion is weaker and is limited to the proximal three-fourths of the tarsus exclusive of the hypotarsus. There is very little insertion on the posttarsal fascia and none distal to metatarsal I. In *Vultur* the insertion is on the distal two-thirds of the tarsus. A wide line on either lateral ridge is the main insertion, but there is also strong fascial insertion and attachment to the foot pads.

Action.—This complex of muscles is the strongest extensor of the tarsus. At the same time due to the origins of the pars externa and media it is effective in flexing the shank upon the femur. Its contribution to the tibial cartilage is important since this structure forms a pulley to hold the other flexor tendons in place and to provide an adjustable surface for their action across the joint. In addition, M. gastrocnemius aids in maintaining the foot pads in an optimal position and may even flex the proximal phalanges of the fore toes.

Comparison of the entire complex.—Various points of difference have already been discussed in the treatment of the separate muscles. Table 41 reveals that M. gastrocnemius is largest in *Coragyps* and smallest in *Gymnogyps* and *Cathartes*. The smaller M. gastrocnemius in *Gymnogyps* results chiefly from a reduced pars interna. Thus, in this genus contraction of the muscle may also cause slight abduction of the lower limb since the pars interna with its origin on the patellar tendon and caput tibiae is weaker.

The point at which the main tendon is formed is also important. In *Coragyps* and *Sarcoramphus* this occurs about two-thirds of the way distally on the shank; this distance is three-fourths to four-fifths in *Cathartes*, four-fifths in *Gymnogyps* and one-half in *Vultur*. Formation of long tendons and more proximal placement of the muscle bulk are well-known adaptations for better terrestrial locomotion.

Previously it has been pointed out that the insertion of M. gastrocnemius is strongest in *Vultur*, *Sarcoramphus* and *Coragyps* and is equally distal in these three and *Cathartes*. The insertion is weakest and most proximal in *Gymnogyps*.

Consequently, considering all the variations mentioned, one must conclude that this muscle complex is by far the best adapted for rapid walking or running in *Coragyps*. It

is much more poorly developed in *Gymnogyps*. In *Cathartes* the adaptation is somewhat better, and in *Sarcoramphus* and *Vultur* the modification for better locomotion is midway between that in *Coragyps* and *Cathartes*.

M. PERONEUS LONGUS

Description.—Two-thirds of the way distally on the tibia the muscle narrows abruptly to form a tendon that continues down the outer face of the lower tibia, across the external side of the tibiotarsal joint, through a cartilage canal on the side of the hypotarsus, and part way down the tarsus. Near its origin the muscle is in close contact with M. tibialis anterior and M. flexor perforans et perforatus digiti III (figs. 18 and 19).

Origin.—The main origin is fleshy from the anterior and lateral surfaces of the outer cnemial crest, but it also arises from the rotular crest and the external face of the inner cnemial crest (fig. 28). In some instances muscle fibers come directly from the pars interna of M. gastrocnemius.

Insertion.—The chief insertion is on the lateral edge of the tendon of M. flexor perforatus digiti III about one-third of the way down the tarsus. There is, however, another tendon of the same size which branches off shortly above the tibial cartilage and runs obliquely posteriorly to its attachment on the anteroproximal corner of the tibial cartilage (fig. 19).

Innervation.—Approximately one-fourth to one-half of the way distally on the tibia a twig of the prefibular branch of the peroneus nerve comes from beneath M. peroneus brevis lateral to M. tibialis anterior and enters the central part of the belly.

Action.—Because of its direct insertion on the tendon of M. flexor perforatus digiti III an important function is flexion of the third toe. At the same time the tarsus is extended, and abducted (as far as the joint allows) due to the passage of the tendon across the lateral face of the joint. The large size of the short tendon to the tibial cartilage indicates that another function is to pull this cartilage proximally when the tarsus is extended.

Comparison.—In *Cathartes* the origin as described above is mainly tendinous. In addition, there is a fleshy origin from the lateral crest of the fibula from the point of insertion of M. extensor ilio-fibularis to the tip of the fibular spine. The muscle is not as wide proximally; it does not cover any of M. flexor perforans et perforatus digiti III. A tendon is formed three-fourths of the way down the shank.

The tendon in *Gymnogyps* is formed just above the tarsal joint, and at the same point there is a wide (1.5 cm.) vinculum with the tibial cartilage. The long tendon passes through a weak tendinous loop on the lateral face of the hypotarsus.

M. peroneus longus in *Vultur* shows considerable deviation from the description given above. In the proximal one-third of the belly M. tibialis anterior is in intimate contact with it; in fact, this latter muscle originates in part from the inner surface of M. peroneus longus. The proximal two-thirds of the anterior edge take some origin from a wide but thin aponeurosis which comes from the inner surface of the tibia and covers the medial edge of M. tibialis anterior. Along its posterior edge there is considerable origin from the lateral crest of the fibula in its distal one-half. The attachment to the tibial cartilage is the strongest of any cathartid examined. Besides the insertion in the middle third of the tarsus, a small tendon attaches to the distolateral corner of the hypotarsus.

In *Sarcoramphus* the belly is three-fourths the length of the tibia, and the origin is entirely tendinous. The muscle is connected to M. tibialis anterior and has a vinculum and accessory tendon as in *Vultur*.

Sarcoramphus has the best developed M. peroneus longus; it is nearly twice as large as in any other cathartid. In *Coragyps* and *Cathartes* the muscle is similarly developed (table 41). An important variation is that in *Coragyps* and *Vultur* the bulk of the muscle lies more proximally on the limb.

Mitchell (1913:1039-1072) in his study of the peroneal muscles of birds found that M. peroneus longus is much smaller than M. peroneus brevis in the Vulturidae and Falconidae. The reverse is true in the Cathartidae. In *Pandion* and the owls examined he found no M. peroneus longus. He concludes that in the Falconiformes except *Pandion* there has been a gradual reduction or specialization of M. peroneus longus and a gradual increase in size of M. peroneus brevis. Since M. peroneus longus is larger in the cathartids and since they probably arose from the Old World vultures it is more likely that reduction has occurred in M. peroneus brevis of New World vultures.

M. TIBIALIS ANTERIOR

Description.—The long, pennate belly of this muscle extends three-fourths of the way down the anterior face of the tibia before gradually forming pure tendon just above the tibial malleoli (fig. 19). The belly lies on the rounded anterior surface of the tibia. Shortly after the tendon is formed it passes through a tendinous loop on the anterior side of the tibia where it is the most superficial. After passing between the malleoli it goes across the tarsal joint and disappears almost immediately beneath the other tendons.

Origin.—The origin of the anterior head (fig. 28) is fleshy from a narrow line on the anterior face of the cnemial crest extending from the outer face of the cnemial crest to its external face. The posterior or femoral head takes tendinous origin from a pit on the most distal part of the external femoral condyle just lateral to the rotular groove (fig. 27). The round slender belly coming from this origin passes distally between the fibular head and the outer cnemial crest to its fusion with the belly of the anterior head in the second quarter of the tibial length.

Insertion.—The inserting tendon is bifurcated and goes down between the other tendons to attach to a rounded tubercle centrally located in the proximal part of the anterior tarsal fossa just distal to the pneumatic foramina (fig. 19).

Innervation.—The anterior head receives a single twig from the peroneus nerve which passes through the tendinous loop for M. extensor ilio-fibularis. The femoral head receives three peroneal twigs—one proximal and one distal to the twig serving the anterior head and one from the same twig as that of the anterior head.

Action.—This is the most powerful flexor of the tarsus. Extension and slight abduction of the lower leg result from action of the femoral head.

Comparison.—In *Cathartes* the two heads do not fuse until two-thirds of the way down the tibia. In *Vultur* and *Sarcoramphus* the anterior head may have some fibers originating from the aponeurosis that extends from the tibia to M. peroneus longus. Otherwise the muscle, except for size, is identical in the genera dissected. The muscle is largest in *Vultur* and smallest in *Gymnogyps;* it is equal and intermediate in *Sarcoramphus, Coragyps* and *Cathartes.* The only modifications of adaptional significance are the variations in relative size and in point of insertion. Ratios of power arm to work arm are: *Gallus* (16.6), *Gymnogyps* (19.1), *Cathartes* (14.9), *Coragyps* (13.9), *Vultur* (19.0), *Pandion* (34.1), *Sarcoramphus* (18.0), and *Aquila* (23.8). The distance from the proximal end of the tarsus to the insertion is used as the power arm. Total length of the tarsus is considered the work arm.

As Hudson (1937:30) points out, the double origin and insertion of this muscle suggests two muscles fused only in the middle of their lengths. Especially is this true in *Cathartes* where fusion of the two heads occurs far distally on the shank. However, in the cathartids the tendons which are often hardly separable insert side by side horizontally, not vertically as figured by Hudson (op. cit., p. 105) for *Bubo virginianus.*

M. FLEXOR PERFORANS ET PERFORATUS DIGITI II

Description.—The upper third of the belly is in intimate contact with the underlying M. flexor perforans et perforatus digiti III; some muscle fibers even arise from the originating tendon of this muscle. The belly narrows suddenly to form a narrow flat tendon which courses obliquely distally and medially along the medial side of M. flexor per-

forans et perforatus digiti III (fig. 19) and crosses the tarsal joint in its own cartilaginous canal. Approximately halfway down the tarsus it takes up a more medial position on the posterior surface of the tarsus and goes beneath the tendon of M. flexor perforatus digiti II. As it passes over the trochlea for digit II it becomes much broader and thicker and perforates M. flexor perforatus digiti II at the latter's insertion on the base of the first phalanx. Almost immediately (in the first third of phalanx 1) it is perforated by the tendon of M. flexor digitorum longus.

Origin.—Fleshy from the distal part of the lateral surface of the external femoral condyle (fig. 27) and tendinous from the proximal part of the same region and from the lower femoral and tibial parts of the tendinous loop for M. extensor ilio-fibularis. It is closely connected to the patellar cap by fascia. There may or may not be some origin from the posterior surface of M. flexor perforans et perforatus digiti III.

Insertion.—The chief point of insertion is on the ventral side of the base of phalanx 2 of digit II. There may be a few tendinous fibers and some strong fascial attachment to the distal ventral surface of phalanx 1.

Innervation.—A laterally directed twig of the tibialis trunk, which enters the shank musculature between the pars externa and pars media of M. gastrocnemius, goes to the middle of the medial side of the belly immediately distal to the inserting tendon of M. extensor ilio-fibularis.

Action.—Flexion of the index digit and extension of the tarsus.

Comparison.—In *Cathartes* and *Vultur* the insertion is on the distal tip of phalanx 1 and few fibers extend on to phalanx 2. In *Cathartes* and in *Gymnogyps* the belly is narrow and extends halfway down the tibia. In *Vultur* the entire origin is tendinous and is only from the external condyle proximal to the lateral femorotibial ligament. In *Gymnogyps* part of the origin is as in *Vultur*, but there is also fleshy origin from the tendon of origin of M. flexor perforans et perforatus digiti III.

In *Gymnogyps* perforation of M. flexor perforatus digiti II is decidedly unequal, that is, there is only a small tendon from the latter muscle that goes medial to M. flexor perforans et perforatus digiti II at the point of perforation. In *Vultur* M. flexor perforatus digiti II is not perforated at all!

Table 41 shows the relative development of this muscle. Little can be said of adaptational modifications. Restriction of the fleshy part of the muscle to the upper part of the shank is the most apparent in *Coragyps*, *Sarcoramphus* and *Vultur*, but the tendinous condition of the muscle in *Vultur* and its more proximal insertion in *Cathartes* and *Vultur* are also important.

M. FLEXOR PERFORANS ET PERFORATUS DIGITI III

Description.—The long, rounded belly of this pennate muscle lies in the center of the outer side of the shank and extends down two-thirds the length of the tibia (fig. 19). After crossing the tarsal joint in the medial superficial group the tendon assumes a central position on the posterior surface of the tarsus deep to the gastrocnemius tendon.

Above the trochlear region of the tarsus there is a vinculum or tendinous connection (only slightly smaller than the main tendon) with the tendon of M. flexor perforatus digiti III. The tendon passes over the trochlea for digit III beneath the tendon of M. flexor perforatus digiti III, and it perforates the latter in the first third of the proximal phalanx. It continues distally as a superficial tendon on the ventral surface of the toe and is itself perforated in the middle of the second phalanx.

Origin.—Part of the origin is tendinous from the lateral part of the external femoral condyle in company with the other toe flexors (fig. 27). This portion is more or less fused with the external femoral and tibial parts of the ilio-fibularis loop. The lateral surface of the patellar tendon, the external face of the proximal outer cnemial crest, the fibular head and the lateral edge of the middle half of the fibula in the region of the insertion of M. extensor ilio-fibularis are also points of tendinous origin. The proximal part of the origin surrounds the tendon of M. ambiens.

Insertion.—Tendinous on the proximal ventral surface of phalanx 3 of digit III. There may also be some fascial attachment to the distal tip of the second phalanx.

Innervation.—An extension of the twig of M. tibialis that goes to M. flexor perforans et perforatus digiti II enters the medial surface between the first and second thirds.

Action.—Flexion of the third digit and extension of the tarsus. At the same time the tibia is flexed upon the femur, and the lower leg may be slightly abducted.

Comparison.—Length of the muscle and its point of insertion are the most variable features. In *Cathartes* and *Gymnogyps* the muscle is three-fourths as long as the tibia, and the insertion is on the distal end of the second phalanx or on the fascia over the joint between phalanges 2 and 3 of digit III. The muscle is confined to the upper half of the tibial length in *Vultur*. There is close attachment to M. flexor perforans et perforatus digiti II, and the only insertion is on the middle ventral surface of phalanx 2.

The muscle is similar in *Coragyps* and *Sarcoramphus*, but in the latter the perforation by a branch of M. flexor digitorum longus occurs in the middle of phalanx 1, not phalanx 2.

The muscle is somewhat smaller in *Gymnogyps* and *Sarcoramphus* than in the other cathartids (table 41).

M. FLEXOR PERFORATUS DIGITI IV

Description.—This spindle-shaped, pennate muscle is situated on the posterior surface of the shank (figs. 19 and 20). The belly has much fascial connection with Mm. flexor perforatus digiti III and IV. At the point where the belly ends about two-thirds of the way down the tibia it is encased medially and posteriorly by the lower belly of M. flexor perforatus digiti III. The tendon goes over the tarsal joint, surrounded anteriorly and on the sides by the tendon of M. flexor perforatus digiti III. Below the tarsal joint the tendon continues distally on the posterolateral corner of the tarsus.

Origin.—Although there is tendinous origin from the central part of the popliteal area of the femur and fleshy origin from part of the popliteal region, the main origin is from the tendinous sheet overlying the posterior surface of M. flexor hallucis longus.

Insertion.—After the tendon widens and thickens as it passes over the trochlea for the fourth toe, it forms three branches at the distal tip of the trochlea. The inner branch inserts on the inner proximal end of phalanx 1 of digit IV. The external branch inserts on the distal, ventrolateral end of phalanx 1, and the median branch inserts on either ventral corner of the distal end of the third phalanx beneath the tendon of M. flexor digitorum longus. The median branch is perforated by and encloses the latter tendon on phalanx 1.

Innervation.—Several twigs of the tibial nerve enter the muscle on its posterior edge. These twigs come from the branch that passes between the bellies of Mm. flexor perforatus digiti III and IV and serves both muscles.

Action.—Flexion of the fourth toe and extension of the tarsus. Due to the weak popliteal origins there is little flexion of the tibia on the femur.

Comparison.—In *Cathartes* a strong tendinous origin from the tendon of origin of M. flexor perforans et perforatus digiti III is present. Distally the inner branch inserts on the distal end of phalanx 3 and the proximal end of phalanx 4; the large median branch inserts on the distal end of phalanx 2.

Gymnogyps shows tendinous origin from the tendons of Mm. flexor perforans et perforatus digiti II and III. The main tendon is perforated by M. flexor digitorum longus *before* the tendon branches. The inner branch inserts on the proximomedial side of phalanx 4; the median branch goes to the proximal part of phalanx 3.

In *Vultur* the belly ends in the middle third of the tibia. The origin is mainly tendinous and is in common with that of M. flexor perforatus digiti III. The tendon of M. ambiens is imbedded in the anterolateral edge of the muscle above the proximal end of the accessory head of M. flexor perforatus digiti III. The inner branch inserts on the

median distal end of phalanx 2, and the external branch attaches to the distolateral surface of phalanx 2 while the median branch (lateral to the tendon of M. flexor digitorum longus) inserts on the proximal lateral corner of phalanx 3.

In *Sarcoramphus* the external branch inserts on the proximolateral end of phalanx 2; the inner branch inserts on the distal surface of phalanx 3, and the median inserts on the proximoventral part of phalanx 3.

The muscle is smallest in *Sarcoramphus* and is significantly smaller in *Coragyps* and *Gymnogyps* than in *Vultur* and *Cathartes*.

M. FLEXOR PERFORATUS DIGITI III

Description.—The symmetrical belly of this muscle forms the posterior border of the middle shank after removal of the superficial layer (figs. 19 and 20). Throughout most of its length, but especially near the origins, the anterior face is closely attached to M. flexor perforatus digiti IV. However, the origins are separated by a branch of the tibial nerve. The bulk of the muscle lies in the middle of the tibial length and forms its tendon at the beginning of the last quarter of the tibia. The tendon extends distally on the midposterior face of the shank and through the central part of the tibial cartilage.

In the last one-fourth of the tibia an accessory tendon from a separate head joins the main tendon (fig. 20). This accessory head is relatively small and lies entirely within the third quarter of the tibia, anterior and external to the point at which the common tendon is formed.

Shortly after fusion of the tendons, the common tendon encloses the anterior, medial and lateral surfaces of M. flexor perforatus digiti IV. The fused tendon is the widest in this region except for the tendon of M. gastrocnemius. At a variable position, but usually in the upper half of the tarsal length, the tendon of M. flexor perforatus digiti III is joined by a strong tendon from M. peroneus longus.

I found no malleolar vinculum between the tendons of Mm. flexor perforatus digiti III and IV, but there is a vinculum given off on the external side of M. flexor perforatus digiti III just above the trochlea. This passes a short distance posteroventrally to fuse with the tendon of M. flexor perforans et perforatus digiti III which lies lateral to M. flexor perforatus digiti IV. Both these latter tendons are partly enclosed by the tendon of M. flexor perforatus digiti III. As the tendon passes over the trochlea for the third toe it becomes broader and thicker. Almost immediately (opposite base of phalanx 1) it is perforated by M. flexor perforans et perforatus digiti III and a branch of M. flexor digitorum longus.

Origin.—The origin of the main head is tendinous from the proximal popliteal area and fleshy and tendinous from the posteromedial face of M. flexor perforatus digiti IV (fig. 20). It has essentially a common tendon of origin with this latter muscle. The accessory head arises tendinously from the posterior surfaces of M. flexor hallucis longus and M. flexor perforatus digiti IV in the middle of the tibial length.

Insertion.—Tendinous on the proximal ventral surfaces of the malleoli of the distal end of phalanx 1 of digit III. Fascial attachment to the entire ventral surface of this phalanx is very strong.

Innervation.—This muscle is served by the same branch of the tibialis nerve as is M. flexor perforatus digiti IV. The nerve enters the musculature between these two muscles in the second quarter of the tibial length and continues down the posterior side of the tibia between them. The accessory head receives the most distal twig of the lateral tibial nerve.

Action.—Flexion of digit III along with extension of the tarsus and weak flexion of the tibia.

Comparison.—In *Cathartes* the accessory head is deep to M. flexor perforatus digiti IV and is considerably longer; it extends proximally to the middle of the tibia and distally into the last fifth of the tibia. Its origin is more complex since it takes origin by

tendon from the popliteal area in company with the tendon of the main head and from the lateral face of the external condyle as well as from the tendon of M. ambiens. In one specimen the accessory head appeared to be a direct continuation of M. ambiens. In this genus the insertion is sheathlike about the distal third of the basal phalanx. Hudson (1937:41) states that the muscle is single in *Cathartes*, yet I found an accessory head in each of the five cathartid genera I dissected.

In *Gymnogyps* the accessory head originates tendinously from the posterior face of M. flexor digitorum longus. There may be some origin from the tendon of M. ambiens which perforates the upper part of the main head of M. flexor perforatus digiti III and M. flexor perforatus digiti IV. Insertion is on the ventral surface of the middle of phalanx 1 on either side of the tendon of M. flexor digitorum longus.

In *Vultur* the main head is more proximal on the tibia, and the accessory head which is in the middle of the tibial length forms no separate tendon; it attaches fleshily to the deep side of the main belly. Origin of the accessory head includes the tendon of M. ambiens and the outer posterior surface of M. flexor perforatus digiti II which in this case is the continuation of M. ambiens. In the middle of the tarsal length a vinculum with M. flexor perforatus digiti IV is present. On the base of phalanx 1 is a wide, flat tendinous loop which holds the inserting tendon next to the bone. In the other genera studied only strong fascia supports the tendon in this position.

In *Sarcoramphus* the accessory head is fused to the main head for its entire length and takes origin from the same tendon as the main head and M. flexor perforatus digiti IV. The insertion is on the proximal end of phalanx 2 of digit III.

From the foregoing comparison it may be seen that the greatest variation is to be found in the accessory head, especially its origin. As Hudson (1937:41) and Gadow (1891:188) state there is much fusion and intermingling of muscle parts in this area.

This muscle apparently is best adapted for locomotion in *Vultur* as is attested by the more proximal location of the bulk of the muscle, the stronger accessory head without a separate tendon, the vinculum with M. flexor perforatus digiti IV, the tendinous loop on phalanx 1, and the greater size of the belly (table 41). In *Coragyps* it is next best adapted. The more proximal insertion in *Gymnogyps* is significant, since the leverage for flexing the third toe is decreased; insertion on the second phalanx as in *Sarcoramphus* increases the leverage.

M. FLEXOR PERFORATUS DIGITI II

Description.—This small thin muscle on the posterolateral border of the middle of the shank is intimately connected to all the surrounding muscles, and especially to M. flexor perforatus digiti IV near its origin. Medial and anterior to this muscle is M. flexor hallucis longus. Posterior and lateral to it is M. flexor perforans et perforatus digiti III. The postfibular branch of N. peroneus lies near its anterior edge. The distal part of the belly is covered laterally and posteriorly by the accessory head of M. flexor perforatus digiti III. Between the third and fourth quarters of the tibial length is formed a small tendon which is centrally located on the posterior side of the tibia; it is lateral and posterior to the wide tendon of M. flexor hallucis longus. However, above the tibial cartilage it crosses this latter tendon to lie medial to it. In this relative position the tendon of M. flexor perforatus digiti II crosses the tarsal joint in its own semicartilaginous canal. Shortly below the hypotarsus it moves to the medioposterior corner of the tarsus and continues thus across trochlea II.

Origin.—In the upper third of the tibia there is fascial origin from the inner surface of M. flexor perforans et perforatus digiti III. Two major sources of origin are tendinous—the tendinous sheath underlying Mm. flexor perforatus digiti III and IV, and the tendon of M. ambiens which it joins a short distance below the tendinous loop for M. extensor ilio-fibularis. It is almost impossible to separate the origins of Mm. flexor perforatus digiti II, III and IV; all take origin on a common tendon from the popliteal area (fig. 20).

Insertion.—At its insertion on the ventral proximal end of phalanx 1 of digit II the

tendon is perforated by M. flexor perforans et perforatus digiti II and M. flexor digitorum longus.

Innervation.—A twig from the tibial nerve on the posterior surface of the tibia enters M. flexor perforatus digiti II near the center of the belly of M. flexor perforatus digiti IV.

Action.—Flexion of digit II and extension of the tarsus. In some instances this muscle may act as a tendon of insertion for M. ambiens.

Comparison.—In *Cathartes* there is little or no connection to the tendon of M. ambiens; this tendon goes to the accessory head of M. flexor perforatus digiti III. Insertion in one specimen was limited to the lateral side of the middle of phalanx 1. In *Gymnogyps* the tendon may or may not be perforated near its insertion; in all instances the main insertion is on the lateroventral side of the base of phalanx 1. The belly of the muscle is much higher in *Vultur*, and its tendon is deep on the extreme medial part of the tibial cartilage. The inserting tendon is not perforated and inserts only on the lateroventral corner of the base of phalanx 1, digit II. In this same genus the muscle has its own tendon from the popliteal area; it is medial to the common tendon of origin of Mm. flexor perforatus digiti III and IV. The ambiens tendon perforates the anterolateral corner of the muscle belly. Some fibers originate from it, but this origin is slight.

In *Sarcoramphus* the insertion is halfway out phalanx 1 of digit II.

Hudson (1937:40) found that the origin in *Cathartes* and *Falco*, among others, is partly from the tendon of M. ambiens. Also, he found that "In many birds the attachment is on the outer side of the proximal end of the first phalanx, and the tendon is not very definitely perforated by the two other flexors" and further, "The tendon is not perforated at all in *Chen, Cathartes, Buteo, Falco* . . . ." Consequently, I assume that the differences in origin and in perforation of the tendon in *Cathartes* show that these features are variable within a genus.

The muscle is 50 per cent larger in *Gymnogyps* and *Vultur* than in the other three cathartid genera. This variation in size and the variation in the point of insertion are the two modifications of adaptational significance. A more lateral insertion, as found in the large condors, causes some abduction of the digit which in turn produces a wider foot for better balance. Origin from the tendon of M. ambiens is important since it adds this muscle to the mechanism effective in flexing the digit.

M. FLEXOR HALLUCIS LONGUS

Description.—The belly is partly pennate near the proximal end. This powerful muscle originates from two heads which are closely connected by fascia (fig. 23). The medial head joins the lateral head near the insertion of M. extensor ilio-fibularis, but it continues fleshy along the medial side of the tendon to a point approximately halfway down the tibia. Here it rather abruptly forms a tendon which fuses to the tendon of the lateral head.

The common tendon courses distally in the midposterior section of the lower tibia, but it veers laterally to run through the central part of the tibial cartilage lateral and superficial to the tendon of M. flexor digitorum longus. Halfway down the tarsus the tendons of M. flexor digitorum longus and M. flexor hallucis longus fuse and continue down the central posterior surface of the tarsus. In the distal part of the tarsus the tendon broadens gradually, and just above the articulation of metatarsal I it gives rise to four branches. The largest branch goes to digit III. Smaller but approximately equal branches go to digits II and IV. The branch to digit I is less than one-half as large as the branch to digit II.

A large tendon (the last vestige of M. lumbricales?) comes off the deep side of the common tendon just before it branches. This tendon inserts on the cartilage pulley overlying the base of trochlea 3.

Origin.—The lateral head arises fleshy from a small spot on the ventral proximal corner of the external femoral condyle (fig. 27) on the tendinous sheet common to the

lateral-lying toe flexors. The medial head arises fleshy from the inner proximal part of the popliteal area slightly proximal to the origin of the lateral head.

Insertion.—After perforating the other toe flexors the tendons continue distally on the ventral surface of the phalanges. Each time a tendon crosses an articulation between phalanges it increases in width. The main tendon on each toe inserts on the ventral proximal base of the claw. On toe II there are small tendons attaching to the distal ventral ends of phalanges 1 and 2. The third toe has two small tendons inserting on the same part of phalanges 2 and 3. On toe IV two small tendons attach similarly to phalanges 3 and 4.

The insertion is in common with M. flexor digitorum longus due to the fusion of tendons in the tarsal region. Garrod (1875) studied the deep plantar tendons in many birds. He found that only in passerines and in *Botaurus* were the tendons of Mm. flexor hallucis longus and flexor digitorum longus separate. In all others a more or less well developed vinculum connects the two tendons in the distal half of the tarsus. In *Coragyps atratus* and *Sarcoramphus* [*Vultur*] *gryphus* he discovered complete fusion a third of the way down the tarsus. Hudson (1937: 48, 108, plate 26) has surveyed the bird groups and found some type of connection between the tendons in all except the Passeriformes and *Upupa*. The vinculum is usually directed downward from the hallux tendon to the tendon of M. flexor digitorum longus. Consequently, contraction of M. flexor hallucis longus flexes all the digits, but tension in M. flexor digitorum longus does not affect digit I. The complete fusion in the vultures preclude separate action by either muscle.

Innervation.—A twig of the medial branch of N. tibialis enters the medioposterior edge just below the fusion of the two heads.

Action.—Entirely in common with M. flexor digitorum longus. All four toes are flexed and adducted simultaneously. At the same time the large size of these muscles makes extension of the tarsus an important function. The tibia is flexed by the lateral head. Because of the origin of M. lumbricales from the common tendon, regulation of the position of the pulley over the third trochlea is possible. In fact, the placing of the pulley in an optimal position for flexion of the third toe is automatic.

Comparison.—Although the origins are from the same general area, they vary greatly individually and generically. In *Cathartes* the two heads arise at the same level, and the lateral head is fleshy as in *Coragyps*, but it also has a tendinous origin from the entire distal rim of the popliteal area. The medial head is partly tendinous on the medial side of the popliteal region, as in *Gymnogyps* and *Sarcoramphus*. In *Vultur* the lateral head originates fleshy and has no connection to the tendons of origin of other toe flexors. The entire fleshy part of the muscle lies in the upper third of the shank in *Vultur*.

In *Sarcoramphus* there are not separate tendons for the two heads.

Points of insertion vary in detail only. As Hudson (1937:48) has pointed out, the number and placement of these fibroelastic tendons of insertion on the phalanges probably are of little taxonomic importance. However, a greater number of such attachments and a more distal insertion indicate a better mechanism for flexing the toes. In *Cathartes* the tendon to the hallux is very small; it is approximately one-fourth as large as the tendon to digit II. In *Gymnogyps* the tendon inserting on digit I is encased by the tendon of M. flexor hallucis brevis. On digit II there are three small tendons to phalanx 2 but none to phalanx 1. In *Gymnogyps*, in addition to the insertion described for the fourth toe of *Coragyps* there is a branch to the proximal ventral surface of phalanx 4. In *Vultur* there are three tendons to digit IV, which insert on the distal midventral ends of phalanges 2, 3, and 4.

The largest inserting branch in *Sarcoramphus* goes to digit II, the next largest to digit III. The branches to digits I and IV are much smaller and approximately equal in size.

M. FLEXOR DIGITORUM LONGUS

Description.—The belly tapers distally to form a tendon four-fifths of the way down the shank (figs. 20 and 23). For its entire length the belly is divided by a tendon that is continuous with the inserting tendon which is a little larger than that of M. flexor

hallucis longus. Just above the tibial malleoli the tendon passes beneath the tendon of M. flexor hallucis longus. As it passes through the tibial cartilage in its own calcified canal it is on the medial side and lies much deeper than the tendon of M. flexor hallucis longus. Approximately halfway down the tarsus the tendon passes laterally to a position beneath the tendon of M. flexor hallucis longus and fuses with it.

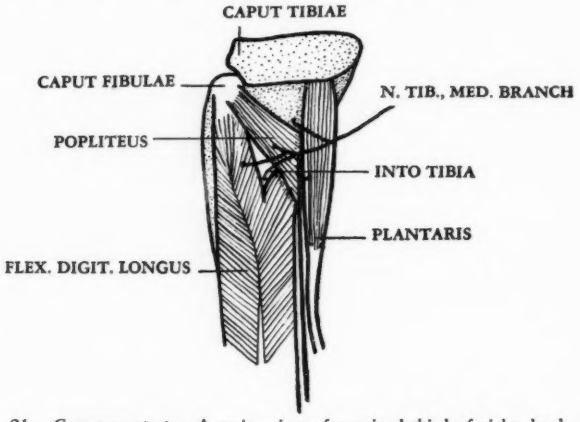


Fig. 21. *Coragyps atratus*. Anterior view of proximal third of right shank, showing innervation of the deep muscles, ×1.

Origin.—The lateral head comes fleshy from the posterior side of the fibula for the entire length of this bone. The medial head arises fleshy from the posterior inner surface of the tibia deep and distal to M. popliteus (fig. 21). It is separated from the belly of M. plantaris posteriorly by blood vessels and branches of the tibial nerves. The two heads become confluent almost immediately.

Insertion.—As described for M. flexor hallucis longus.

Innervation.—From tibial nerve but there may be some peroneal innervation of the medial part (fig. 21).

Action.—Same action as described for M. flexor hallucis longus except this muscle does not flex the femorotibial joint.

Comparison.—Table 41 shows that the two major toe flexors just discussed are best developed in *Sarcoramphus*, *Gymnogyps* and *Cathartes*. The combined volume is relatively least in *Coragyps* and slightly larger in *Vultur*.

In *Cathartes* the origin of the lateral head is more extensive, but the medial head is reduced. In *Gymnogyps* and *Sarcoramphus* the origin covers all of the tibia posterior to the fibula, from M. popliteus to the distal quarter of the tibia. The origin in *Vultur* is as in *Gymnogyps* except that it extends only two-thirds of the way down the shank. Thus it may be observed that these two muscles show little variation.

M. LUMBRICALES

Description.—This much reduced semitendinous muscle is situated in the lower third of the posterior surface of the metatarsus immediately anterior to the common inserting tendon of Mm. flexor hallucis longus and flexor digitorum longus. As it passes distally it becomes wider, but it is in all instances covered by the tendon just named.

Origin.—By tendon and fascia from the anterior surface of the inserting tendon of

Mm. flexor hallucis longus and flexor digitorum longus proximal to the branching of this tendon.

Insertion.—Mixed fleshy and tendinous on the proximal end of the cartilaginous pulley over trochlea 3.

Innervation.—A twig from the peroneus nerve which runs down the posterior surface of the tarsus lateral to M. flexor hallucis brevis.

Action.—Serves to pull the third and perhaps the fourth trochlear pulleys posteriorly when the toes are flexed. Mechanically, flexion of toe III is possible, but the muscle is too weak to have much effect.

Comparison.—The muscle in *Coragyps* appeared to be almost entirely tendinous and thus could have no action except that imparted to it by action of the muscles on whose tendon it originates. In the other cathartids the muscle is definitely fleshy. It is equally developed in *Cathartes* and *Gymnogyps*, but it is smaller and bandlike in *Vultur* and *Sarcoramphus*.

M. POPLITEUS

Description.—M. popliteus is a short, but relatively wide, fleshy muscle lying on the proximal anterior surface of the tibia. From the point of origin it passes medially and distally to its insertion. It is somewhat wider and thicker near the insertion. Hudson (1937:51) found that ". . . the fibular and tibial attachments are usually directly opposite as in *Bubo* . . . ." but in *Sula*, *Chen*, *Totanus*, *Larus* and *Chordeiles* the direction is as in the Cathartidae (fig. 21).

Origin.—Chiefly fleshy from the posteromedial corner of the fibular neck (fig. 21).

Insertion.—Fleshy on the posteromedial corner of the tibia beneath the upper part of the belly of M. plantaris. The proximal end of the insertion is at the same level as the distal end of the origin.

Innervation.—The branch of the tibial nerve serving M. plantaris and M. flexor digitorum longus sends a twig to this muscle which lies between two other branches of the nerve. The anterior branch goes next to the caput tibiae, and the posterior branch passes between M. flexor digitorum longus and the tibia and enters a foramen at the distal end of the fibular crest (fig. 21).

Action.—Any action by this muscle is slight due to the strong ligamental binding of most of the fibula; the head is more loosely attached. The muscle would tend to pull the fibular head medially, posteriorly and distally. It may serve to hold the caput fibulae in the fibular groove of the femur when the tibia is rotated inward and forward as the bird "toes in."

Comparison.—The volumetric ratios in table 41 are subject to considerable error due to the smallness of the muscle, but they indicate that the muscle is best developed in *Gymnogyps* and *Cathartes*. In *Coragyps* the muscle is smallest. The larger size in the first two may be correlated with their more pronounced "pigeon-toed" stance on the ground if the main function of the muscle is as suggested.

In *Vultur* the muscle is almost horizontal. In all other respects the muscle is identical in the cathartids.

M. PERONEUS BREVIS

Description.—In the last quarter of the tibia it forms a strong tendon that passes alone obliquely caudally across the tibia just above the malleoli. At this point it widens and sends a small tendon to the tibial cartilage (fig. 20). The main tendon continues distally on the external face of the tibial malleolus and is held in place by strong fascia that forms a band across it.

Origin.—Fleshy from the anterior and lateral surfaces of the distal third of the fibula and form a narrow area on the tibia anterior to the fibular spine and extending distally from the end of the spine (fig. 28).

Insertion.—By a small tendon on the external anteroproximal corner of the tibial

cartilage and by a strong tendon on the externoproximal corner of the hypotarsus (fig. 20).

Innervation.—From a twig of the peroneus nerve trunk which passes along the anterior edge of the fibula (fig. 20).

Action.—Any action of this muscle is slight. Abduction of the metatarsus is the chief function, but extension of the metatarsus is also possible. Because of the insertion on the tibial cartilage the muscle aids M. plantaris in retracting this mass and, secondarily, in extending the metatarsus.

Comparison.—The fleshy portion in *Cathartes* and *Gymnogyps* extends distally almost to the end of the tibia. In the latter I could find no tendon to the tibial cartilage, but there was much strong fascial contact. The muscle in *Vultur* is identical with that in *Coragyps*. In *Sarcoramphus* the origin, distally, covers the fibular spine and even takes considerable origin from the lateral surface of the tibia posterior to the fibula.

The muscle is smallest and equally developed in *Coragyps* and *Cathartes;* it is intermediate in size in *Sarcoramphus* and is largest in *Gymnogyps* and *Vultur*.

M. EXTENSOR DIGITORUM LONGUS

Description.—A tendinous band divides this muscle (fig. 20) longitudinally and is continuous with the inserting tendon. Approximately two-thirds of the way down the tibia a strong tendon is formed which passes through a fibrous loop above the malleoli in company with the tendons of M. tibialis anterior and other toe flexors. Almost immediately after emerging from the fibrous loop the tendon passes alone through a bony canal just proximal to the internal condyle. From here it courses across the medial face of the internal condyle covered superficially by nerves and blood vessels. In the upper part of the tarsus it is medial and superficial, but distally it moves laterally to follow metatarsal III down to the trochlea for digit III. The tendon is medial to the insertion of M. tibialis anterior and in this region passes through a wide semitendinous loop.

Above trochlea 3 the tendon widens greatly and subsequently divides into three branches. At the point of division there is much fascial attachment to the cartilaginous pulleys of trochlea 2, 3 and 4. The tendon to the third toe is the largest of the three branches, and the tendon to digit II is somewhat larger than the one to the fourth toe.

Origin.—Fleshy from the median half of the anterior surface of the tibia, narrowing gradually as it goes distally (fig. 28).

Insertion. On digit II.—The tendon runs across the anterolateral corner of trochlea 2 and continues along the dorsal surfaces of the phalanges to its main insertion on the dorsal part of the base of the claw. As the tendon passes distally, it becomes broader. Opposite the middle of phalanx 1 a small branch turns medially to insert on the dorsomedial corner of the base of phalanx 2.

On digit III.—This branch is intimately connected to the branch to digit IV until it is opposite the midanterior face of trochlea 3. It then proceeds distally through the anterior groove of trochlea 3, through a small tendinous loop near the base of phalanx 1, and immediately divides. The inner branch inserts partly on the distal end of phalanx 1 but sends a very small tendon along the medial surfaces of phalanges 2 and 3 to insert on the dorsomedial corner of the base of the claw. The lateral and more superficial branch widens extensively opposite the distal end of phalanx 1, and its medial part inserts on the median, proximal part of phalanx 2. Its lateral portion continues across the lateral surface of the base of phalanx 2 as two small, yet distinct, tendons which fuse half way out the phalanx and widen to form a tendinous sheath entirely covering the dorsal surface of phalanx 2. On the deep side there is an attachment to the cartilage overlying the articulation between phalanges 2 and 3. At the distal end of phalanx 2 a tendon (one-half the size of the main tendon) comes off medially and courses along the median face of phalanx 3 in company with the small tendon already described in that position. These two small tendons are distinct to the point of insertion on the claw. The

main branch continues from the distal end of phalanx 2 as a broad flat tendon which inserts on the base of the claw. Throughout the length of phalanx 4 the tendon is intimately connected to the phalanx by fascia.

On digit IV.—The tendon runs across the anteromedial portion of trochlea 4 and continues distally on the dorsal surfaces of the phalanges to insert on the dorsal surface of the base of the claw. In the genus being discussed (*Coragyps*) I could not find the branches described by Hudson (1937:31), but strong fascia attaches this tendon to the dorsal surfaces of the bases of phalanges 2, 3 and 4.

Innervation.—From the branch of N. peroneus that passes anteriorly (external to tendon of M. ambiens and the fibula) across the anterolateral surface of the tibia above the fibular crest (fig. 20).

Action.—This is a major extensor of digits II, III and IV. Simultaneously the tarsus is flexed upon the shank.

Comparison.—In *Cathartes* the fleshy part of the muscle is three-fourths as long as the tibia. The inserting tendon is smaller, and its branch to digit II is smaller than the branch to digit IV. The tendon to the second toe passes through a small loop on the dorsal base of phalanx 1; it is much weaker than in *Coragyps*. The insertion on digit III is variable; in some instances at the distal end of the third trochlea a small branch passes at right angles to the main tendon and inserts on the base of phalanx 1 of digit IV. On digit III there is no median branch of the lateral tendon opposite the distal end of phalanx 2, and there is only weak fascial attachment to the claw. Although the tendon to the fourth toe is large proximally, in the middle of phalanx 1 it narrows abruptly to a very small tendon. Points of insertion on digit IV are: base of phalanx 1 (chief insertion), lateral proximal face of phalanx 2, median proximal surface of phalanx 3 and dorsal proximal part of phalanx 4.

The belly of the muscle ends three-fourths of the way down the shank in *Gymnogyps*. The origin is wider and is two-thirds as long as the tibia. Although there is much fascial attachment to the joint between phalanges 1 and 2 of digit II, the real insertion is on the claw only. On digit III the inner branch inserts only on the dorsal base of phalanx 2 while the outer branch inserts broadly on the dorsal and medial surfaces of the same phalanx; a small branch of this outer branch extends distally on either side of phalanx 3 to insert on the dorsal base of the claw. The main tendon of digit IV passes out the dorsolateral surface of the phalanges to insert on the base of the claw. Opposite the base of phalanx 2 a wide tendon branches off medially and inserts on the dorsomedial surface of the distal one-half of phalanx 2; a similar branch comes off at the base of phalanx 3 and inserts on the same part of phalanx 3.

In *Vultur* the insertion on the second toe is the same as in *Coragyps* except there is a broad attachment to the dorsum of the proximal part of phalanx 2. On digit III the insertion is as in *Gymnogyps* with the exception that the median branch formed opposite the distal end of phalanx 1 inserts strongly on the proximal end of phalanx 2 as well as on the distal end of phalanx 1. The lateral branch formed opposite the distal end of phalanx 2 inserts widely all along the anterolateral surface of phalanx 3, and passes to the anterior and lateral surfaces of the base of the claw as in *Coragyps*. The chief insertion on digit IV is on the claw, but there is a strong connection with the proximal end of phalanx 3 and with the entire anterior surface of phalanx 4.

In *Sarcoramphus* the belly is four-fifths the length of the tibia. In addition to the insertion on digit II as described for *Coragyps* there is a median tendon which inserts on the middle of phalanx 1. On digit IV the tendon does not reach to the claw, but spreads out over basal half of phalanx 4 as a wide fascial attachment.

The ratios given in table 41 show a remarkably well developed M. extensor digitorum longus in *Cathartes*. Differences between the other genera are small; this muscle is apparently least developed in *Coragyps*.

Aside from the variation in the length of the belly, the only differences are in the mode of insertion, and these are minor. The muscle belly in *Coragyps* and *Vultur* is

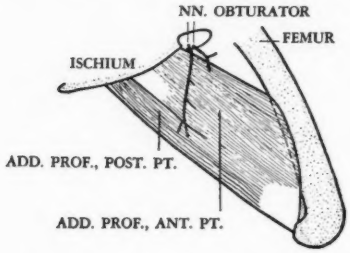


Fig. 22. *Coragyps atratus*. Lateral view of the right thigh showing M. adductor profundus, ×1/2.

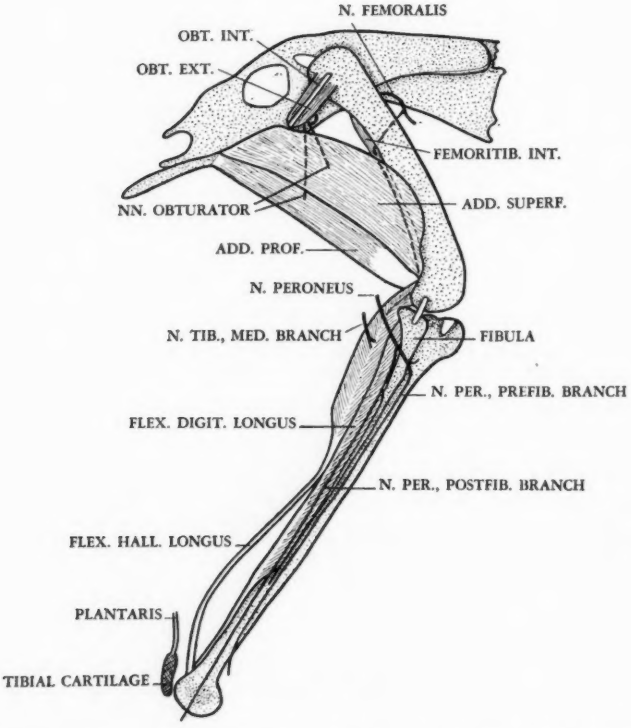


Fig. 23. *Coragyps atratus*. Lateral view of the right leg showing the deep layer of muscles, ×1/2.

two-thirds as long as the tibia; it is three-fourths of the tibial length in *Cathartes* and *Gymnogyps* and four-fifths in *Sarcoramphus*. Variations in manner of attachment to digit II are minor, but there is greater similarity between the insertions here in *Coragyps*, *Sarcoramphus* and *Vultur* than between these three and *Cathartes* and *Gymnogyps*, which are similar. It is also important that in *Coragyps*, *Sarcoramphus* and *Vultur* the areas of insertion are larger and the tendons are bound more tightly to the phalanges. The manner of insertion on digit III is greatly variable generically and individually. The absence of any insertion on the claw on the fourth toe in *Sarcoramphus* is of major functional significance. In *Coragyps* and *Vultur* the attachments to digit IV are stronger and more distal; in *Cathartes* the main insertion on this digit is on the base of phalanx 1!

M. PLANTARIS

Description.—This is a long slender muscle lying on the posteromedial surface of the tibia immediately anterior to the medial edge of M. flexor perforatus digiti III (fig. 21). One-third to one-half way down the tibia the belly gradually gives rise to a small tendon that courses down the posteromedial corner of the tibia. Just above the tibial malleoli the tendon turns laterally to enter the extreme medial part of the tibial cartilage.

Origin.—Fleshy from a rather extended area on the posteromedial corner of the tibial shaft immediately distal to the inner articular area of the caput tibiae (fig. 21).

Insertion.—Tendinous on the proximal medial part of the tibial cartilage (fig. 23).

Innervation.—A twig from the medial branch of N. tibialis enters the middle of the posterolateral edge of the belly.

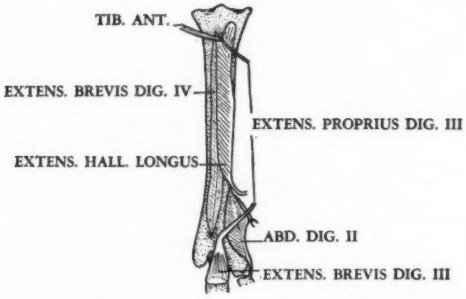


Fig. 24. *Coragyps atratus*. Anterior view of the right tarsometatarsus showing the short muscles, ×1/2.

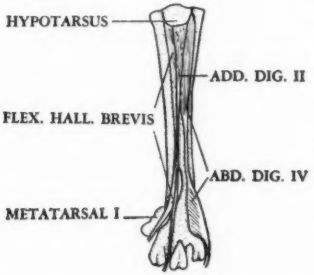


Fig. 25. *Coragyps atratus*. Posterior view of the right tarsometatarsus showing the short muscles, ×1/2.

Action.—Weak extension of the tarsus is possible, but the main function of this muscle is to move the tibial cartilage proximally into the optimum position for the action of the tendons of the tarsal extensors and toe flexors. Thus it aids in preventing the crushing of the tendons (Gadow, 1891:186) when the tarsus is extended.

Comparison.—The muscle in the cathartids is similar in structure. It is best developed in *Gymnogyps* and least developed in *Sarcoramphus* and *Coragyps*. In *Cathartes* and *Vultur* the muscle is intermediate in size.

Gadow (1891:186) states that the muscle is lacking in all diurnal and nocturnal birds of prey and parrots. Hudson (1937:37-38) did not find it in *Buteo*, *Bubo* and *Otus*, but he states that it is strong and typical in *Falco* and *Cathartes*. It was well developed in the cathartid vultures.

M. EXTENSOR PROPRIUS DIGITI III AND M. EXTENSOR BREVIS DIGITI III

Description.—Hudson (1937:54) found only one short extensor muscle attached to the third toe; he chose to call this the M. extensor proprius digiti III. Gadow (1891: 199) has found both the above named muscles well developed and separate in the ratites. In the Cathartidae the two muscles are present, but they are not separate, and M. extensor proprius digiti III is represented chiefly by a slim tendon (fig. 24); there may be a few short muscle fibers near the insertion of M. tibialis anterior. The tendon forms part of the origin of M. extensor brevis digiti III. The two muscles will be considered together.

Origin.—Tendinous and fleshy from a small spot on the anterior surface of the tarsus surrounding the insertion of M. tibialis anterior and fleshy from a triangular area on the anterior surface of the base of trochlea 3 (fig. 24).

Insertion.—Tendinous on the anterior surface of the base of phalanx 1, digit III.

Innervation.—It was impossible to determine the innervation (if any) of the remaining vestiges of M. extensor proprius digiti III. The lateral branch of N. peroneus serves the M. extensor brevis digiti III.

Action.—Weak extension of the third toe.

Comparison.—In *Cathartes* and *Gymnogyps* the tendon is practically nonexistent, and there are no muscle fibers on the proximal part of the tarsus. In some specimens of *Cathartes* the tendon was absent. No tendon is present in *Vultur*, and the M. extensor brevis digiti III is small and handlike.

M. EXTENSOR HALLUCIS LONGUS

Description.—Three-fifths of the way down the tarsus the belly turns medially and forms a small tendon on the inner side of the tarsus one centimeter above the proximal end of metatarsal I (fig. 24). On the median side of the tarsus the flat tendon is held tightly in place by strong fascia overlying it. The fascia continues across the metatarsal I and to the base of phalanx 1. Hudson (1937:51) ascribes an elasticity to this fascia which enables it to act as an automatic extensor of the hallux, antagonistic to M. flexor hallucis longus. In my preserved specimens I was unable to determine the elasticity of this fascia.

Origin.—Fleshy from the medial part of the anterior tarsal groove (fig. 24). The chief area of origin is medial and proximal to the double tendon of insertion of M. tibialis anterior; few fibers arise distal to the proximal fifth of the tarsus.

Insertion.—Tendinous on the anterior surface of the base of phalanx 2.

Innervation.—A twig from the medial branch of the peroneus nerve enters the upper half of the belly.

Action.—Extension of the hallux. If the fascia is elastic, as Hudson states, and produces a certain amount of extension when unopposed by M. flexor hallucis longus this muscle may only act to produce the maximal amount of extension.

Comparison.—In *Vultur* and *Gymnogyps* the belly turns medially halfway down the tarsus. In *Cathartes* the belly is much longer than in *Coragyps;* it extends out two-thirds the length of metatarsal I. The main insertion in the turkey vulture is on the anterior

surface of the distal half of phalanx 1, but a small tendon inserts on the base of this phalanx.

In *Sarcoramphus* the tendon is formed halfway down metatarsal I.

The M. extensor hallucis longus is best developed in *Cathartes* and *Gymnogyps;* it is approximately one-third as large in the other three genera. The smallness in *Coragyps* may in part be the result of the greater amount of fascia surrounding the tendon of insertion and the reduced size of the first toe. Essentially the same may be said in the case of *Vultur,* but here the abbreviated muscle is probably the result of the much reduced digit. The more proximal insertion in *Cathartes* limits the power of the larger muscle present in this genus but provides for greater speed of action; scarcity of elastic fascia may account for the increased size of the muscle.

M. ABDUCTOR DIGITI II

Description.—See figure 24.

Origin.—Fleshy from the anterior side of metatarsal I and from the anteromedial surface of metatarsal II at the level of metatarsal I and extending well down the trochlea for digit II (fig. 24).

Insertion.—The tendon which is formed opposite trochlea 2 passes medial to the trochlear surface and inserts on the medial side of the base of phalanx 1, digit II.

Innervation.—By a medial branch of N. peroneus.

Action.—Abduction of the second toe. There may be some slight extension at the same time. The fibers originating from metatarsal I pull digit I forward.

Comparison.—Table 41 indicates that the muscle is exceptionally well developed in *Gymnogyps;* in this form the muscle origin does not extend into the distal third of the length of metatarsal I. Consequently the effective action on digit I is reduced. The muscle is weakest in *Coragyps.* In *Sarcoramphus* the origin extends laterally to the middle of metatarsal III in the same area as on metatarsal II. As in *Vultur* there is considerable origin from the medial face of metatarsal II. The muscle in this genus is half the relative size it is in *Gymnogyps* but is larger than in *Vultur, Cathartes* and *Coragyps.* In *Vultur* the muscle is in two parts; the lateral part lies next to the medial edge of M. extensor brevis digiti IV and takes some fleshy origin from metatarsal III. The medial part is about one-fifth the size of the lateral part and takes origin exclusively from the anterior surface of the entire length of the first metatarsal. The origin of the lateral division extends medially on to the inner surface of the second metatarsal. Thus in *Vultur* the more lateral placement of the main bulk of the muscle plus the origin on the medial surface of metatarsal II make a better mechanism for abduction of digit II. Therefore, the difference between the effectiveness of the muscles in *Vultur* and *Gymnogyps* is less than is indicated by their volumes. One would expect to find more abduction of digit II in these large birds and in *Sarcoramphus* than in *Cathartes* and *Coragyps.* Spreading of the toes provides a better foundation for balancing the body.

M. EXTENSOR BREVIS DIGITI IV

Description.—Its pennate structure is best seen in the lower part of the muscle since only a few fibers are present in the proximal third of the tarsus. Just before entering the intermetatarsal space (foramen), the muscle narrows abuptly to form a tendon (fig. 24).

Origin.—Fleshy on a line lying just inside the lateral ridge of the anterior tarsal groove (fig. 24).

Insertion.—After emerging from the intermetatarsal space between trochlea 3 and 4 the tendon goes distally on the median surface of the fourth trochlea and inserts on the proximal end of the inner surface of phalanx 1, digit IV.

Innervation.—A twig from the lateral branch of N. peroneus enters the proximal half of the belly.

Action.—Adduction of the fourth toe. I can not see how any extension of the digit is possible as Hudson (1937:54) states, except from an extreme flexed position. This

muscle probably comes into play as the foot is raised from the ground. At this time the toe is flexed forward to a maximal degree. An extending action by this muscle aids slightly in raising the foot on the fourth toe, but its chief function is pulling the fourth toe in toward the main axis of the foot to reduce the possibility of catching the toe on obstructions.

Comparison.—Structurally the muscle is similar in the cathartids. It is best developed in *Cathartes* and *Gymnogyps*, intermediate in *Sarcoramphus* and weakest in *Vultur*. Reduction of the size of the muscle in *Coragyps* and *Vultur* is correlated with reduction of the fourth digit as an adaptation for better locomotion on the ground.

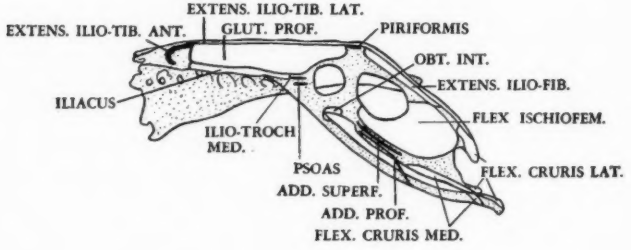
M. ADDUCTOR DIGITI II

Description.—See figure 25.

Origin.—Fleshy from the lateral half of the distal face of the hypotarsus and from a triangular area on the surface of the tarsus immediately distal to the middle of the hypotarsus (fig. 25).

Insertion.—Tendinous on the lateral surface of the base of phalanx 1, digit II.

Innervation.—A twig from the postfibular branch of N. peroneus enters the muscle on the deep surface in the middle of the belly.



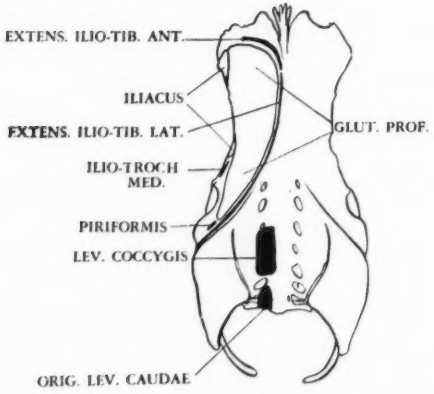


Fig. 26. *Coragyps atratus*. The synsacrum showing attachments of muscles, ×½.

Action.—Adduction of the second toe is the first result of contraction of this muscle; when adduction is complete the toe is weakly flexed. As in the case of M. extensor brevis digit IV and M. flexor hallucis brevis this muscle probably is of use only in the recovery stroke of the leg.

Comparison.—The muscle is similar in New World vultures, but in *Cathartes* the insertion is farther ventrally and thus provides a better opportunity for flexion. In *Gymnogyps* this muscle is relatively largest; it is smallest in *Coragyps* and *Vultur*.

M. FLEXOR HALLUCIS BREVIS

Description.—This small, slim muscle lies on the inner posterior corner of the tarsus. In the middle of the tarsus there are few muscle fibers, but above metatarsal I a small belly is developed. The muscle is pennate, and the tendon is confined to its medial edge in the distal three-fourths of the muscle (fig. 25).

Origin.—Fleshy from a line along the medial side of the posterior tarsal groove (fig. 25).

Insertion.—Tendinous on the proximal posterior edge of phalanx 1 of digit I. Opposite the first metatarsal it is medial to the tendon of M. flexor hallucis longus and is perforated by it.

Innervation.—A small branch of the postfibular branch of N. peroneus passes beneath the middle of the belly of M. adductor digiti II, and a twig enters the deep, lateral edge of the muscle.

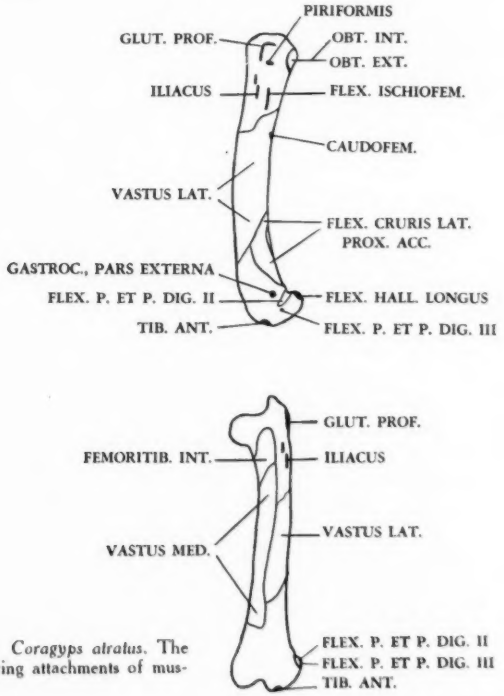


Fig. 27. *Coragyps atratus*. The femur showing attachments of muscles, ×½.

The main part of the branch continues distally beneath the medial edge of M. adductor digiti II, and a twig enters the middle of the superficial surface of the more distal belly.

Action.—Weak flexion of the first toe. Adduction posteriorly of digit I is the chief function.

Comparison.—In *Cathartes* the belly is wider, longer and is not interrupted in the middle of the tarsal length. The tendon to the point of insertion is much larger than in *Coragyps*. The origin in *Sarcoramphus* is much wider proximally and extends proximally as far as the proximal face of the hypotarsus. In *Vultur* and *Gymnogyps* the muscle is not constricted as much in the middle of its length as it is in *Coragyps*. In *Gymnogyps* there is in addition to the usual insertion a wide fascial attachment to the connective tissue surrounding the articulation of the metatarsal and phalanx 1 of digit I. There is much strong fascial connection to the entire posterior surface of the first phalanx in *Vultur* and *Sarcoramphus*. The muscle is strongest in *Gymnogyps* and is intermediate in *Sarcoramphus;* it is weaker and about equally developed in the other genera.

M. ABDUCTOR DIGITI IV

Description.—This is the most lateral of the small post-tarsal muscles; the upper belly is situated just inside the ridge forming the lateral border of the posterior tarsal groove. The more distal belly is found immediately proximal to the trochlea for digit IV. Throughout its length the tendon is lateral to the bellies of the muscle and goes distally across the midexternal face of trochlea 4 (fig. 25).

Origin.—Fleshy from the proximal end of the tarsus lateral to the hypotarsus and extending down to the proximal face of the fourth trochlea (fig. 25).

Insertion.—Tendinous on the external face of phalanx 1, digit IV approximately one-third of the distance out this phalanx.

Innervation.—Twigs from the postfibular branch of N. peroneus which traverses the full length of the muscle enter the superficial surfaces of the two bellies.

Action.—Strong abduction of the fourth digit.

Comparison.—The only variation in this muscle is in the point of insertion. In *Gymnogyps* the insertion is on the ventrolateral part of the base of phalanx 1. In *Vultur* and

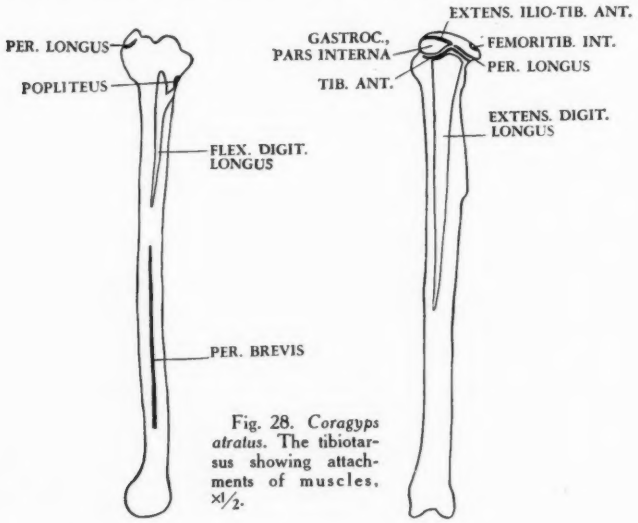


Fig. 28. *Coragyps atratus*. The tibiotarsus showing attachments of muscles, ×1/2.

Sarcoramphus it is on the lateral surface of the base of the same phalanx. *Gymnogyps* possesses the best developed muscle; in *Vultur* and *Sarcoramphus* it is approximately one-half as large. The muscles are equally developed in *Coragyps* and *Cathartes*.

M. ADDUCTOR DIGITI IV

I found no traces of this muscle in the New World vultures. Hudson (1937:58) found that it was the most poorly defined and rudimentary of all the muscles connected with the hind limb. He found it fleshy only in *Phasianus colchicus*. Gadow (1891:204) found the muscle in a few forms only—*Rhea*, *Bucorvus* and *Rhamphastus*.

TABLE 41.—Ratios of the Volume of Individual Muscles to Total Volume of Hind-limb Muscles*.

	Cathartes	Coragyps	Gymnogyps	Vultur	Sarcoramphus
Exten. ilio-tib. lat.	3.83	9.60	4.90	5.90	6.50
Extens. ilio-tib. ant.	4.83	3.73	3.70	3.70	3.69
Piriformis	0.83	0.11	0.15	0.12	0.04
Gluteus profundus	6.17	4.75	7.96	6.86	4.52
Iliacus	1.17	0.91	1.12	1.02	0.95
Ilio-troch. medius	0.33	0.11	0.15	0.12	0.09
Vastus lateralis and Vastus medialis	7.67	8.82	9.69	8.43	6.50
Gastrocnemius	13.16	16.98	12.27	14.44	13.78
Peroneus longus	5.16	5.32	7.41	6.67	13.33
Tibialis anterior	5.33	5.21	3.91	6.13	5.10
Extens. ilio-fibularis	7.67	6.34	7.77	7.00	5.62
Flexor p. et p. dig. II	1.50	1.36	1.22	1.04	1.02
Flexor p. et p. dig. III	3.50	3.51	2.99	3.39	2.66
Flexor perf. dig. IV	2.67	2.04	2.03	2.50	1.91
Flexor perf. dig. III	2.67	2.15	2.49	3.35	1.86
Flexor perf. dig. II	0.67	0.68	1.02	1.02	0.67
Flexor digitorum longus and Flexor hallucis longus	5.33	3.97	5.43	4.39	5.55
Popliteus	0.25	0.11	0.30	0.20	0.18
Flexor cruris lateralis	8.83	8.72	6.04	8.28	8.45
Flexor cruris medialis	3.00	1.91	2.38	2.25	2.80
Peroneus brevis	0.17	0.17	0.46	0.43	0.31
Extens. digitorum long.	2.50	0.79	0.96	1.11	1.00
Plantaris	0.50	0.34	0.71	0.48	0.36
Flexor ischiofemoralis	2.41	1.81	2.08	0.97	2.00
Adductor superficialis	4.17	2.94	4.82		3.47
Adductor profundus	1.80	2.94	3.05	6.47	2.67
Ambiens	0.33	0.68	0.36	0.65	0.58
Femoritibialis int.	1.20	2.04	1.32	1.33	1.47
Extens. prop. dig. III and Extens. brev. dig. III	0.08	0.05	0.05	0.02	0.04
Extens. hallucis longus	0.33	0.11	0.30	0.12	0.13
Abductor dig. II	0.17	0.10	0.41	0.14	0.20
Extens. brevis dig. IV	0.33	0.11	0.30	0.06	0.20
Adductor dig. II	0.08	0.05	0.15	0.06	0.08
Flexor hallucis brevis	0.08	0.17	0.70	0.20	0.44
Abductor dig. IV	0.17	0.17	0.46	0.22	0.24
Obturator internus	1.08	1.13	1.12	1.02	1.20
	98.9	99.8	99.5	99.9	98.7

* The following muscles were not included in the computation of total volume: M. caudofemoralis, M. psoas, M. obturator externus and M. lumbricales.

Table 42.—Synonymy of the Muscles of the Hind Limb.

Shufeldt, 1890	Gadow, 1891	Hudson, 1937	Howell, 1938	Fisher
gluteus medius	ilio-trochantericus posterior	ilio-trochantericus posterior	gluteus profundus	gluteus profundus
gluteus minimus	ilio-trochantericus anterior	ilio-trochantericus anterior	iliacus	iliacus
.....	ilio-trochantericus medius	ilio-trochantericus medius	.....	ilio-trochantericus medius
.....	ilio-femoralis externus	glutaeus medius et minimus	piriformis	piriformis
.....	ilio-femoralis internus	iliacus	psoas	psoas
.....	ambiens	ambiens	ambiens	ambiens
sartorius	ilio-tibialis internus s. sartorius	sartorius	extensor ilio-tibialis anterior	extensor ilio-tibialis anterior
gluteus primus	ilio-tibialis	ilio-tibialis	extensor ilio-tibialis lateralis	extensor ilio-tibialis lateralis
vastus externus	femori-tibialis externus	femori-tibialis externus	vastus lateralis	vastus lateralis
cruraeus	femori-tibialis medius	femori-tibialis medius	vastus medialis	vastus medialis
vastus internus	femori-tibialis internus	femori-tibialis internus	.....	femori-tibialis internus
femoro-caudal	caud-ilio-femoralis	piriformis	caudofemoralis	caudofemoralis
semitendinosus	caud-ilio-flexorius	semitendinosus	flexor cruris lateralis	flexor cruris lateralis

flexorius

lateralis

lateralis

semimembranosus	ischio-flexorius	semimembranosus	flexor cruris medialis	flexor cruris medialis
biceps flexor cruris	ilio-fibularis	biceps femoris	extensor ilio-fibularis	extensor iliofibularis
obturator externus	ischio-femoralis	ischio-femoralis	flexor ischiofemoralis	flexor ischiofemoralis
obturator internus	obturator	obturator internus	obturator	obturator internus
gemellus	accessorii M. obturatoris	obturator externus	.....	obturator externus
adductor longus	pub-ischio-femoralis	adductor longus et brevis, pars anterior	adductor superficialis	adductor superficialis
adductor magnus	pub-ischio-femoralis	adductor longus et brevis, pars posterior	adductor profundus	adductor profundus
tibialis anticus	tibialis anticus	tibialis anterior		tibialis anterior
extensor longus digitorum	extensor digitorum communis	extensor digitorum longus		extensor digitorum longus
peroneus longus	peroneus superficialis	peroneus longus		peroneus longus
tibialis posticus	peroneus profundus	peronaeus brevis		peroneus brevis
gastrocnemius	gastrocnemius	gastrocnemius		gastrocnemius
soleus	plantaris	plantaris		plantaris
flexor perforatus indicis primis pedis	flexor perforatus digiti II	flexor perforatus digiti II		flexor perforatus digiti II
flexor perforatus medius primus pedis	flexor perforatus digiti III	flexor perforatus digiti III		flexor perforatus digiti III
flexor perforatus annularis primus pedis	flexor perforatus digiti IV	flexor perforatus digiti IV		flexor perforatus digiti IV

Table 42.—Synonymy of the Muscles of the Hind Limb—Continued.

Shufeldt, 1890	Gadow, 1891	Hudson, 1937	Howell, 1938	Fisher
flexor perforatus indicis secundus pedis	flexor perforans et perforatus digiti II	flexor perforans et perforatus digiti II		flexor perforans et perforatus digiti II
flexor perforatus medius secundus pedis	flexor perforans et perforatus digiti III	flexor perforans et perforatus digiti III		flexor perforans et perforatus digiti III
flexor perforans digitorum profundus	flexor profundus s. perforans	flexor digitorum longus		flexor digitorum longus
flexor longus hallucis	flexor hallucis longus	flexor hallucis longus		flexor hallucis longus
.....	popliteus	popliteus		popliteus
extensor hallucis brevis	extensor hallucis brevis	extensor hallucis longus		extensor hallucis longus
.....	extensor proprius digiti III	extensor proprius digiti III		extensor proprius digiti III
.....	extensor brevis digiti III	extensor brevis digiti III		extensor brevis digiti III
.....	extensor brevis digiti IV	extensor brevis digiti IV		extensor brevis digiti IV
.....	abductor digiti II	abductor digiti II		abductor digiti II
flexor brevis hallucis	flexor hallucis brevis	flexor hallucis brevis		flexor hallucis brevis
.....	adductor digiti II	adductor digiti II		adductor digiti II
.....	flexor brevis digiti III	lumbricales		lumbricales

Correlation of Variations in Myology with Differences in the Use of the Leg

The ratio of the total volume of the leg muscles to the weight of the bird gives a rough indication of the development of the leg musculature. These ratios for a single individual of each genus are: *Gymnogyps* (17.1), *Cathartes* (14.3), *Sarcoramphus* (27.8), and *Coragyps* (19.7). The ratio for *Vultur* is higher than that for *Coragyps,* but no weight was available for the individual dissected. Thus the muscles of the leg constitute a greater per cent of the body weight in *Sarcoramphus* and *Vultur* than in the other genera.

Volumes of individual muscles and their relation to the total volume of muscles operating the leg (table 41) are more significant; however, the ratio of the volume of muscles to the body weight against which they act is also significant.

Placement of the bulk of the muscles on the limb is significant; it is well known that cursorial forms possess shorter-bellied muscles with longer tendons than do slow moving forms. These muscles are more proximally situated, which eliminates weight at the distal end of the limb which must be swung through a wide arc in locomotion.

Shapes of individual muscles of the shank indicate that the bulk of the musculature is more proximally situated in *Coragyps, Sarcoramphus* and *Vultur* than in *Cathartes* and *Gymnogyps.* For example, the belly of M. gastrocnemius which constitutes one-eighth to one-sixth of the volume of the hind limb musculature is limited to the proximal half of the shank in *Vultur,* the proximal two-thirds in *Coragyps* and *Sarcoramphus* and the proximal three-fourths to four-fifths in *Cathartes* and *Gymnogyps.* M. peroneus longus forms a tendon two-thirds of the way down the tibia in *Coragyps* and *Vultur;* in *Cathartes* and *Sarcoramphus* the tendon is formed three-fourths of the way distally on the tibia. In *Gymnogyps* the tendon is formed just above the tibial malleoli. The belly of M. flexor hallucis longus lies in the upper third of the shank in *Vultur;* in the other genera it extends into the distal half of the tibial length. Other muscles show similar differences in location.

Therefore, the placement of the muscles is most advantageous for movements of the hind limb in *Vultur* and is the least advantageous in *Gymnogyps.* In *Coragyps* and *Sarcoramphus* the muscles lie farther proximally than they do in *Cathartes.* The greater bulk located distally in *Gymnogyps* and *Cathartes* decreases their agility on the ground and is a factor in the production of the shuffling gait.

Muscles moving the femur.—These muscles may be classified in two distinct groups, those moving the femur posteriorly and those moving it anteriorly. There are also adductors and abductors of the femur, but as has been mentioned previously these are relatively unimportant because of their small size and because of the semi-fixed position of the femur in the Cathartidae.

The one-joint muscles pulling the femur posteriorly are: Mm. adductor superficialis, adductor profundus, ischiofemoralis, caudofemoralis, obturator externus and obturator internus. The M. caudofemoralis may be eliminated here by reason of its weakness; Mm. ischiofemoralis, obturator internus and obturator externus are relatively insignificant here because of their short lever arm and because their chief function is rotation of the femur. Yet when they are opposed by Mm. gluteus profundus, iliacus and iliotrochantericus medius the action causes flexion posteriorly of the femur.

Ratios of the sum of the volumes of these muscles to total volume of the leg musculature indicate that they are best developed in *Gymnogyps* (11.07 per cent) and next best developed in *Cathartes* (10.46). In *Coragyps* and *Vultur* they are weakest (8.5); in *Sarcoramphus* they are intermediate (9.34 per cent). However, in the discussion of these muscles it was pointed out that certain important modifications have occurred. In *Cathartes* the adductors arise farther anteriorly and their anterior parts are better developed than are the posterior parts. In *Vultur* the muscles are of uniform thickness and originate farther posteriorly; also, the tendinous sheath underlying M. adductor profundus provides a tendinous action not represented in the volume of the muscle. Thus the effectiveness of the muscles in *Coragyps* and *Vultur* is greater than is indicated by their volume.

Certain two-joint flexors, Mm. flexor cruris lateralis, flexor cruris medialis and extensor ilio-fibularis, are also important in flexing the femur posteriorly, and in holding the anterior part of the body upright. If their synergists across the femorotibial joint contract and prevent flexion of the shank most of the action of the muscles would be devoted to posterior extension of the upper leg.

The functions of the muscles in this region are so significant in so many actions—perching, running, jumping and as synergists for muscles originating from the synsacrum and femur and extending the shank—that correlation with differences in a single action is impossible. Miller (1937:25) found this to be true also in the geese he examined.

The muscles flexing the femur anteriorly are: extensor ilio-tibialis anterior, gluteus profundus, flexor ischio-femoralis, iliacus and ilio-trochantericus medius. With the exception of M. extensor ilio-tibialis anterior the above muscles have exceptionally short lever arms and function chiefly in rotation of the femur forward and inward. It is to be expected that forward flexion of the femur is a much less powerful action than posterior flexion in birds in which most of the movements of the limb occur below the knee.

A comparison of the relative volumes of M. extensor ilio-tibialis anterior in the various genera shows that the muscle is best developed in *Cathartes*, but in this genus the effectiveness of the muscle is decreased by a more proximal insertion. Thus, in M. ilio-tibialis anterior, the only powerful muscle in a position to flex the femur anteriorly, there is little variation among the vultures.

The total volume of muscles rotating the outer surface of the femur forward and inward is relatively greatest in *Cathartes* and *Gymnogyps*. Since

there are no structural differences in these muscles, volume is a good index to action. The strength as indicated by the volume is closely related to the pigeon-toed stance of *Cathartes* and *Gymnogyps* when standing or walking slowly. M. flexor ischiofemoralis is the only antagonist of the forward and inward rotators of the femur that varies in relative volume among the cathartids. The better development of this muscle in *Cathartes* and *Gymnogyps* is probably a result of the need for a mechanism to eliminate the pigeon-toed gait for more successful locomotion on land. It is logical that increased development should occur in this external, more superficial muscle than in the deeper obturators which are more limited by bone and overlying muscles. Its insertion is farther distally and thus the muscle is more effective than the obturators.

One would expect M. caudofemoralis, a still more superficial and freer muscle, to have increased in size if it functions in rotation of the femur. As suggested previously, however, it is chiefly concerned with movements of the tail. Yet, in *Cathartes* it is three times as large relatively as in *Coragyps;* the muscle is absent in the two condors and the king vulture. Thus *Cathartes,* due to better development of M. ischiofemoralis and M. caudofemoralis, is more able to eliminate the pigeon-toed gait. This is one factor in the more agile ground locomotion of the turkey vulture as compared to the California condor.

M. extensor ilio-tibialis lateralis and M. piriformis are the two muscles in a position to abduct the femur; the former functions chiefly in extension and abduction of the shank. M. piriformis is best developed in *Cathartes* in which it is approximately five times as large as in any other vulture. Thus although abduction of the femur is slight in any New World vulture, *Cathartes* possesses a somewhat better means of abduction.

Possible adductors of the femur are: M. ambiens, M. psoas, part of M. adductor profundus and M. flexor cruris medialis; such action of the two latter muscles is negligible. When the synergists of M. ambiens prevent its acting to flex the toes or to extend the tibia it adducts the entire leg. It is perhaps significant that M. ambiens is almost twice as large relatively in *Coragyps, Sarcoramphus* and *Vultur* as it is in *Cathartes* and *Gymnogyps.* Any development to adduct the limb is significant since it aids in the elimination of a straddled gait.

Muscles moving the tibiotarsus.—Muscles which are primarily concerned with extension of the shank are: Mm. extensor ilio-tibialis lateralis, extensor ilio-tibialis anterior, vastus lateralis, and vastus medialis. The strong femoral head of the M. tibialis anterior is also an extensor of the tibia; M. femori-tibialis internus may aid in extension, but its chief function is forward and inward rotation and adduction of the lower limb. M. ambiens also may extend the shank.

A survey of the total volume of the muscles whose chief function is extension of the shank shows that extension is most powerful in *Coragyps* in which the muscles constitute 22.8 per cent of the total hind limb musculature. In *Cathartes* and *Sarcoramphus* the per cent is 16.6; in *Gymnogyps* and *Vultur* it is 18.6.

Development of muscles extending the shank is significant as regards terrestrial locomotion; greater development is correlated with greater ability to climb, jump and run. The forward thrust of the tibia in these activities is important in determining speed of locomotion and length of stride. Absence of structural modifications in shank extensors indicates that the volume of the muscles, which is an index to their power, is the chief adaptation. Better development of these muscles in *Coragyps* is a major factor in its greater agility and speed on the ground.

Tibial flexors include: pars externa and pars media of M. gastrocnemius, extensor ilio-fibularis, flexor cruris lateralis and flexor cruris medius. Total relative volumes of these muscles in the various cathartid genera are: *Cathartes* (19.50), *Coragyps* (16.97), *Sarcoramphus* (16.87), *Gymnogyps* (16.19) and *Vultur* (17.53). Volumes of components connected with the gastrocnemius are not included. The chief flexors, M. extensor ilio-fibularis and the M. flexor cruris muscles, are also closely related to posture and weight of the bird, as suggested previously. Consequently increased volumes of the muscles may result from many factors and are not a simple index to the ability to flex the shank

Differences in attachments must be considered. The M. extensor ilio-fibularis originates farther anteriorly and the tendinous loop is shorter in *Cathartes* and *Gymnogyps*. Although the area of insertion is in approximately the same position as regards the length of the tibia, the tibia has lengthened somewhat in *Coragyps* and *Vultur* and greatly in *Sarcoramphus*. The first modifications decrease the efficiency of the muscle in *Cathartes* and *Gymnogyps;* the second may increase the speed at which the distal end of the tibia moves posteriorly in *Sarcoramphus, Coragyps* and *Vultur*.

M. flexor cruris lateralis originates much farther distally in *Vultur, Sarcoramphus* and *Coragyps;* consequently its efficient vector of force is greater. The larger size of M. flexor cruris medius in *Cathartes* is largely offset by a more proximal insertion which shortens the lever arm.

The modifications discussed above when considered in view of the relative volumes demonstrate much weaker tibial flexion in *Gymnogyps* than in any other cathartid. *Vultur* and *Sarcoramphus* apparently possess the best mechanism for flexion of the shank. The difference between the black vulture and the turkey vulture is more obscure. *Cathartes* exhibits greater work capacity, but the muscles are less advantageously placed. It is impossible to calculate the balance of these factors; however, I think the apparatus in *Coragyps* is better adapted for terrestrial locomotion.

Another group of muscles which is not ordinarily considered as important in tibial flexion is the toe flexor assemblage originating from the femur. Although the action of any individual muscle is slight the importance of the flexion produced by the entire group can not be denied. If flexion of the toes is prevented by antagonistic muscles extending the toes these flexors extend the tarsus and flex the tibia. Similarily, if the flexion of the toes is prevented and

tarsal extension is prevented by contraction of M. tibialis anterior the action of these flexors is limited to flexion of the tibia.

Total relative volume of the four muscles (Mm. flexor perforans et perforatus digiti II, III, and flexor perforatus digiti III and IV) originating at least partly on the femur demonstrates that their work capacity is least in *Sarcoramphus;* it is greatest in *Vultur* and *Cathartes*. Although the differences suggested by these volumes are none too reliable due to the variety of action possible in these muscles they are of value in adding to the picture of tibial flexion as given above.

The adductors of the tibia include the Mm. flexor cruris medius, ambiens and femoritibialis internus. Adduction of the shank is the chief function of only M. femoritibialis internus; the action of M. ambiens in adducting the limb has been discussed previously, and adduction of M. flexor cruris medius is inseparably associated with flexion of the shank.

M. femoritibialis internus is appreciably longer in *Vultur*. Consequently its length of action is greater. Relative volumes of this muscle (table 41) reveal that it is much better developed in *Coragyps* than in any other vulture. The modification in *Vultur* causes the muscle to be more effective than in *Cathartes* and *Gymnogyps*. Thus as regards power to adduct the shank, *Coragyps* and *Vultur,* and probably *Sarcoramphus,* rank righer than the other two genera. This power of adduction is important in keeping the limb beneath the body for more efficient support and locomotion.

M. extensor ilio-tibialis lateralis is the only muscle in a position to abduct the shank except perhaps certain toe flexors which originate on the external femoral condyle. It is impossible to detect differences in the ability to abduct the tibia.

The broad flat articulating surfaces of the proximal end of the tibia and the absence of well developed cnemial crests extending proximally toward the femur provide the basic foundation for rotation of the tibia on the femur .The insertion of M. extensor ilio-fibularis on a raised papilla on the lateral face of the fibula enables it to rotate the outer surface of the shank outward and backward. M. femoritibialis internus opposes this action, rotating the tibia forward and medially. However, it is probable that little rotation actually occurs in the Cathartidae.

Muscles moving the tarsometatarsus.—Two muscles, M. gastrocnemius and M. tibialis anterior, are primarily concerned with movements of the tarsus. In addition to these muscles a number of others (Mm. peroneus longus, flexor perforans et perforatus digiti II, III, flexor perforatus digiti II, III and IV, flexor hallucis longus, flexor digitorum longus and plantaris) aid in extending the tarsus. M. extensor digitorum longus is an important factor in flexing the tarsus. Because of their attachments to the bellies of M. gastrocnemius, M. flexor cruris lateralis and M. flexor cruris medialis may function in extending the tarsus.

M. gastrocnemius is the only muscle acting to extend the tarsus without flexing the digits; even the M. gastrocnemius may aid in digital flexion because of its fascial insertion which in *Vultur* fans out over the sole of the foot and even on to the basal phalanges of the anterior digits. Relative volume of this muscle is greatest in *Coragyps* and next largest in *Vultur;* it is smallest in *Gymnogyps*. Differences in the point and strength of the insertion are significant; in *Cathartes* and *Sarcoramphus* the point of insertion is the same as *Coragyps,* but the lines of attachment are much narrower, indicating a weaker insertion. In *Gymnogyps* the insertion is weaker and more proximally situated; it is limited to the proximal three-fourths of the tarsus and does not extend on to the hypotarsus. In *Vultur* the insertion is the most distally situated; the M. gastrocnemius attaches to the distal two-thirds of the tarsus and extends out beneath the foot pads to the basal phalanges of the anterior toes.

The greater work capacity of M. gastrocnemius in *Coragyps,* as indicated by the greater volume of its belly, and its more distal insertion give the black vulture better ability to extend the tarsus, which in turn makes it more agile on the ground. Its ability to hop and spring more than other vultures probably is in large part due to these structural differences. The turkey vulture is less able to run or walk with powerful strides because, although the insertion is placed like that in *Coragyps,* the work capacity of the muscle is less.

In *Vultur,* as compared to *Gymnogyps,* the distal insertion and better development of the muscle provide more power and a longer power arm. The shorter power arm in *Gymnogyps* permits of greater speed in extension of the tarsus, but the relatively weaker muscle and the great weight of the bird make running a laborious process. The inability of the California condor to hop over small obstructions, to spring from the ground at the end of the takeoff run or to spring into the air from a perch is a result of weakness of this muscle. Further, the slow, dignified walk is resorted to because it does not require rapid or powerful action from M. gastrocnemius.

The differences between *Cathartes* and *Coragyps* and between *Vultur* and *Gymnogyps* demonstrate that development of the muscle and point of insertion are not to be correlated with the size of the bird. They are directly correlated with the ability to run, hop and spring.

It may be argued since the pars externa and pars media function also in tibial flexion that the total volume of M. gastrocnemius is not an indication of the capacity for tarsal extension. Antagonists contracting to prevent tibial flexion probably cause the effect of M. gastrocnemius to be limited to tarsal extension. The writer is aware that muscles seldom act singly, but in a study of this nature the potentialities of muscular action must be the chief subject investigated.

The chief flexor of the tarsus, the M. tibialis anterior, is equally developed in *Coragyps, Sarcoramphus* and *Cathartes*. It is best developed in *Vultur* and is weakest in *Gymnogyps*. The insertion is situated farthest distally on the tarsus in *Gymnogyps, Vultur* and *Sarcoramphus;* it is most proximal in *Cora-*

gyps and only slightly more distal in *Cathartes*. *Vultur* consequently is best adapted for thrusting the tarsus forward in the recovery stroke; the muscle is largest, and its insertion is the most distal. *Gymnogyps*, on the other hand, has an equally distal insertion, but the muscle is only half as large as in *Vultur*. Weak recovery of the limb in *Gymnogyps* causes stumbling over small objects and a shuffling gait. Likewise, this weakness causes the slow walk to be used whenever possible.

Differences between the black and turkey vultures as regards M. tibialis anterior are small, the only significant difference being the more distal insertion in *Cathartes*. Thus, in *Cathartes*, as compared to *Coragyps*, the power arm is longer, but the power to operate the arm is the same. This results in a slower but somewhat more powerful flexion of the tarsus during the recovery stroke in *Cathartes*. For agility on the ground, running and hopping, speed not power is necessary. The shorter lever arm in *Coragyps* together with a muscle equal in size to that in *Cathartes* aids in making the black vulture more adept in terrestrial locomotion.

M. extensor digitorum longus which may aid in flexion of the tarsus is outstandingly larger in *Cathartes*. At first glance this would indicate increased power to flex the tarsus. However, the larger bulk of the muscle apparently is a compensatory development to overcome the effect of the short lever arm on which this muscle acts. In *Cathartes* its chief insertions are on the basal phalanges; they are on the distal phalanges in the other genera.

Abduction of the tarsus, which in any case must be slight, is a possible function of two muscles. M. peroneus longus tends to abduct the tarsus because its tendon to the tendon of M. flexor perforatus digiti III passes across the lateral face of the tarsal joint; it is twice as large in *Sarcoramphus* as in any other cathartid. M. peroneus brevis functions chiefly in abduction of the tarsometatarsus. It is smallest and equally developed in *Cathartes* and *Coragyps*, intermediate in *Sarcoramphus* and in *Gymnogyps* and *Vultur* it is largest.

Muscles moving the digits.—Analysis of the function and interaction of muscles attached to the toes is difficult. The long flexors are intimately connected in the upper half of the tibia and at their points of origin; one tendon may fuse with another or a vinculum may be present. The action of muscles passing over two or more joints is complex and without physiological experiments it is impossible to state what the muscles actually do. We can, however, note what their capabilities are.

The possible action of the long toe flexor muscles in flexing the tibia and extending the tarsus has been discussed above. If we assume that the synergistic action of other muscles may prevent tibial flexion and tarsal extension and may cause the total action of the muscles to be effective in flexing the digits the sum total volume of the flexor muscles may be an index to the ability to flex the toes. The ratios of the total volume of the flexor muscles to the total volume of the muscles of the leg are: *Cathartes* (16.3), *Coragyps* and *Sarcoramphus* (13.7), *Gymnogyps* (15.2) and *Vultur* (15.7). The difference between *Cathartes* and *Coragyps* and between *Coragyps* and *Gymnogyps* is important.

Greater size of M. flexor digitorum longus and M. flexor hallucis longus in the turkey vulture accounts for most of the difference between the turkey vulture and the black vulture. These muscles in *Cathartes* and *Coragyps* are similarly constructed; the insertions in the turkey vulture are somewhat more proximal and do not appear to be as strong as in the black vulture. Consequently the difference in the ability to flex the toes is not as great as the difference in volume might indicate. The larger muscles in *Cathartes* are in part at least a compensation for a shorter lever arm.

In *Vultur*, as compared to *Gymnogyps*, the insertions are stronger and more distal. Since the work capacity of the muscles is essentially the same it must be concluded that *Vultur* can flex the anterior toes more powerfully, but more slowly than the California condor.

Another factor must be considered in the analysis of the differences between the cathartids in the function of M. flexor digitorum longus and M. flexor hallucis longus. Digits I and IV are much reduced in *Vultur*, and they are shorter in *Coragyps* than in *Cathartes*. As a result the action of these muscles is greater on digits II and III which are the important digits in locomotion. Greater ability to flex the fore toes provides more forward thrust on the body as it moves forward in the power stroke of the hind limb. Consequently *Vultur* is better adapted in this regard than *Gymnogyps*, and *Coragyps* is better adapted than *Cathartes*.

M. flexor perforans et perforatus digiti III inserts chiefly on phalanx 2, digit III in *Cathartes, Gymnogyps, Sarcoramphus* and *Vultur;* in *Coragyps* it is on phalanx 3. M. flexor perforatus digiti III inserts on the distal end of phalanx 1, digit III in *Cathartes, Coragyps* and *Vultur;* in *Gymnogyps* it is on the middle of the length of the phalanx, and in *Sarcoramphus* it is on the proximal end of phalanx 2. M. flexor perforatus digiti II inserts on the proximal ventral surface of phalanx 1, digit II in *Cathartes* and *Coragyps* and halfway out the phalanx in *Sarcoramphus;* it inserts on the lateroventral surface of the base of the phalanx in *Vultur* and *Gymnogyps*. In *Coragyps* the inserting tendon of M. ambiens is a direct continuation of the tendon of origin of M. flexor perforatus digiti II; in the other genera the ambiens tendon is intimately connected to most of the toe flexors.

The modifications above reveal that digits II and III in *Coragyps* may be flexed somewhat more powerfully than in *Cathartes*. The more distal insertion of M. flexor perforatus digiti III in *Vultur* as compared to *Gymnogyps* provides for stronger flexion of the third toe. Digit IV possesses a better developed flexing mechanism in *Cathartes* and *Gymnogyps* than in *Coragyps* and *Vultur*.

The single long extensor of the four toes, M. extensor digitorum longus, is best developed in *Cathartes;* it is much weaker in *Vultur, Sarcoramphus* and *Gymnogyps* and is least developed in *Coragyps*. Two modifications in *Cathartes* reduce the efficiency of this muscle; on digit III the insertion on the claw is weak, the main insertion being on phalanges 2 and 3. On digit IV the chief insertion is on the base of phalanx 1 rather than on the claw as in the other

genera. On digit IV in *Sarcoramphus* there is no insertion on the claw. Development of the extensor muscles of the toes is undoubtedly related to weight and length of the digits. Thus in *Cathartes* as compared to *Coragyps* the larger size of the digits and the more proximal insertions necessitate a muscle of greater work capacity to extend the digits.

The heavier digits of the California condor together with the slightly weaker muscle, as compared to *Vultur*, causes toe extension to be less efficient.

Short muscles operating the digits.—Without exception all the short tarsal muscles moving the toes are smaller in *Coragyps* than in *Cathartes* and smaller in *Vultur* than in *Gymnogyps*. The percentages these muscles are of total leg musculature are: *Cathartes*, 2.24; *Coragyps*, 1.72; *Gymnogyps*, 2.79; *Vultur*, 1.64; *Sarcoramphus*, 2.09. The decreased size in *Vultur* and *Coragyps* is partly a reflection of the decreased length of the digits and partly perhaps a result of the need for eliminating weight on the distal end of the locomotor apparatus. The small movements which these muscles are capable of producing are rather insignificant in running forms which depend largely upon the greater movements caused by longer, more proximal muscles with more work capacity and a greater range of action.

The relatively small M. flexor hallucis longus in *Coragyps* and *Vultur* is a direct result of the shortened digit and its lesser use in ground locomotion. The same may be said for M. extensor hallucis longus.

Development of the short abductors and adductors of the toes is significant. Abduction of digit II and digit IV causes the formation of a wider foundation for balanced support of the body weight. Abduction of digit II is caused by two muscles, M. abductor digiti II and M. flexor perforatus digiti II, in *Gymnogyps* and *Vultur;* M. flexor perforatus digiti II does not function as an abductor in the other genera because its insertion is on the ventral, not the lateroventral, surface of the basal phalanx.

The work capacity of these abductors is related to the weight of the bird. M. flexor perforatus digiti II is a half larger in *Gymnogyps* and *Vultur*, and M. abductor digiti II and M. abductor digiti IV are best developed in *Gymnogyps*. M. abductor digiti IV in *Vultur* is stronger than in *Coragyps* and *Cathartes*. Its weakness as compared to *Gymnogyps* is a result of the decreased importance of the fourth toe in *Vultur*.

M. adductor digiti II is three times as large in *Gymnogyps* as in *Coragyps;* it is twice as large as in *Cathartes*. This muscle, as is to be expected, follows the trends of development exhibited by its antagonist, M. abductor digiti II.

The adductor muscles of the toes are not as well developed as are the abductor muscles because many of the long toe flexors produce adduction and because the elastic fascia surrounding the toes aids in keeping them in an adducted position.

General Summary

A comparative study has been made of the locomotor apparatus of the five genera that constitute the family Cathartidae. These New World vultures are: the California condor, *Gymnogyps californianus;* the Andean condor, *Vultur gryphus;* the royal vulture, *Sarcoramphus papa;* the turkey vulture, *Cathartes* aura; and the black vulture, *Coragyps atratus*. Major emphasis has been placed on the adaptive modifications shown by the bones and muscles of the several genera. Wherever possible these differences have been correlated with differences in the use of the wing, tail, and hind limb.

As a corollary, the topographic relationships between the various muscles and their innervations have been worked out to aid in future work on the homologies of avian muscles.

The wing of all cathartids shows modifications which adapt it for soaring, at which all New World vultures excel. The wing is long and broad, and it may be held extended in soaring position for long periods of time .The arrangement of the two-joint flexor and extensor muscles which run from the humerus to the hand is such that the distal part of the wing is automatically extended and held in position by the action of the larger, more proximal muscles. Various muscles are modified to provide better control of the flight feathers. The muscles of the hand are well developed; two muscles, not previously described, were found to furnish additional power to move the index digit and the primaries. Dermal muscles moving the feathers of the wing and holding them in place are strong; some skeletal muscles have dermal fasciculi for movement of the feathers. Muscles which function primarily to tilt the distal parts of the wing show increased size; delicate tilting of the wing is important in soaring birds, for it affects the camber and the angle of incidence of the wing.

Increase in the length of the wing has occurred as a result of lengthening in the distal bony elements and in the primaries. The cathartids possess broad flat articulating surfaces for the metacarpus and the phalanges of the fingers; these articulations permit the rotatory movement which is necessary for successful soaring.

The sternocoracoidal articulation in these vultures allows of little movement, which in turn aids in making the pectoral girdle more rigid. There is, however, no articulating surface between the furculum and the coracoid; they are connected by ligaments only. Fewer ribs articulate with the sternum in the cathartids than in other falconiforms.

Flapping is laborious in all the genera because of the long broad wing which can not be moved up or down with ease and can not be tilted greatly. *Coragyps* is better able to flap than are the other vultures because its wing is shorter and because the proximal muscles of the wing are, in general, relatively larger and possess longer power arms.

The muscles which tilt the entire wing (an action necessary in swift, flapping flight) are relatively larger in *Coragyps* than in the other cathartids.

In the turkey vulture these modifications for flapping flight are not as well developed as in *Coragyps*, but they are more apparent than in the much larger *Gymnogyps* and *Vultur*. The long wing in *Cathartes*, as compared to *Coragyps*, increases the difficulty of flapping flight.

The California condor and the Andean condor possess more powerful distal muscles on the wing than do the black and turkey vultures. This development is correlated with the need of greater movement in the distal parts of the wing because the broad proximal segments are less capable of movement in the condors than in the small vultures.

The greater body weight of *Gymnogyps*, *Vultur* and *Sarcoramphus*, is another factor in the lesser ability of these birds to flap. The ratio of supporting surface of the wing to body weight is greatest in *Cathartes;* this enables the turkey vulture to soar in quiet air when the California condor is becalmed. At the same time it decreases the stability of soaring, since air currents have a relatively greater surface on which to act.

Listed in order of decreasing ability to flap, the genera of the cathartids are: *Coragyps*, *Sarcoramphus?*, *Cathartes*, and *Gymnogyps* and *Vultur*. This is also the order of increasing ability to soar.

In the New World vultures the tail is an important part of the mechanism for soaring and steering. In all the genera the depressor musculature is better developed than is the levator musculature of the tail. As a whole the musculature of the tail is relatively best developed in *Coragyps*, and the rectrices are relatively shortest in this genus. The insertions of the muscles are more medial in the black vulture than in the other cathartids. Larger muscles together with more medial and more proximal insertions in *Coragyps*, as compared to the condors, enable the black vulture to move the tail more powerfully and more rapidly, as in the braking action when the bird comes in for a landing.

Levation of the tail is stronger in *Sarcoramphus*, *Gymnogyps* and *Vultur* than in *Coragyps* and *Cathartes;* this is correlated with the ability to soar, since air currents striking the elevated tail tend to raise the anterior end of the body and thereby increase the angle of incidence and decrease the speed of flight.

The tail muscles in *Gymnogyps*, *Sarcoramphus* and *Vultur* are so placed as to give more delicate control of the rectrices and of the tail as a unit; that is, certain of the muscles insert farther laterally and distally in the condors than in the smaller vultures. *Cathartes* is intermediate between the condors and *Coragyps* as regards the use and structure of the tail.

In the muscles of the hind limb, *Coragyps* and *Vultur* show more modifications for cursorial action than do *Cathartes* and *Gymnogyps*. In the black and royal vultures and the Andean condor the total leg musculature is relatively better developed, the muscles are more proximally situated on the leg, the muscles adducting the leg are larger, the tibial flexors and extensors are relatively larger and are more advantageously situated, as are the flexors and

extensors of the tarsometatarsus, and the muscles moving the digits, especially digits I and IV, are much reduced.

In many leg muscles *Cathartes* exhibits greater adaptations for terrestrial locomotion than does the California condor.

The bones of the leg demonstrate more cursorial adaptation in *Coragyps*, *Sarcoramphus* and *Vultur* than in *Cathartes* and *Gymnogyps*. In these the distal end of the femur is displaced farther medially, the rotular and fibular grooves are deeper and wider and the tibia is longer. The tarsometatarsus is longest in *Sarcoramphus* and *Coragyps*. The tarsometatarsus is narrower and more cylindrical, and digits I and IV are shortest in *Vultur* and *Coragyps*. All the toes are shorter in *Vultur* than in any other genus. *Cathartes*, however, possesses more of the modifications for increased cursorial ability than does *Gymnogyps*.

There are in the cathartids some indications of a graviportal stance; these are the most pronounced in *Gymnogyps*, less in *Vultur*, *Sarcoramphus* and *Cathartes* and least in *Coragyps*. Usually the graviportal stance is correlated with body weight, but in *Vultur*, which probably is heavier than *Gymnogyps*, and in *Coragyps*, which is slightly heavier than *Cathartes*, the graviportal characteristics are obscured and eliminated by the adaptations for greater speed and agility on the ground.

No cathartid vulture is capable of using the foot as an organ for predation. They can not even perch well on objects of small diameter. The proximal phalanges of the toes are too long to permit the extreme flexing necessary to grasp small objects, and the muscles moving the digits are weak.

Garrod (1874) set up various formulae to represent the presence or absence of certain muscles in the thigh of birds, namely, the pars caudofemoralis and the pars iliofemoralis of M. piriformis (M. caudofemoralis), M. semitendinosus (M. flexor cruris lateralis) and M. accessorius semitendinosi (M. flexor cruris lateralis, proximal accessory). Hudson (1937) has amplified Garrod's formulae by considering two additional characters, M. ambiens and the vinculum between the tendons of M. flexor perforatus digiti III and M. flexor perforans et perforatus digiti III.

In his study of the turkey vulture Hudson (1937:66) found the vinculum and all the above muscles, except the pars iliofemoralis of M. caudofemoralis. He used *Cathartes* as an example to describe the condition in the family Cathartidae. On the basis of the present study several points in his characterization of the cathartid muscles must be modified. M. caudofemoralis can not be used as a distinguishing character. The absence of this muscle in three of the five cathartid genera well illustrates the point made earlier that it is undesirable to generalize about a family without studying all the genera in it. Hudson states that M. flexor perforatus digiti II is not perforated; I found it consistently perforated in *Coragyps*, *Sarcoramphus* and *Cathartes*. It may or may not be perforated in *Gymnogyps*, and in a single specimen of *Vultur* it was not perforated. Consequently this perforation can not be used to distinguish the New World vultures from any other group.

Characters not mentioned by Hudson but which were found consistently in the cathartids include: presence of an accessory head for M. flexor perforatus digiti III, which lies in the distal half of the tibial length anterior to the main head; presence of a distal accessory head for M. flexor cruris lateralis, which is intimately associated with the gastrocnemius complex.

Although this study was not designed especially to show relationships within the family, several points of interest may be mentioned. The genera of the family Cathartidae are well developed and distinct; the differences found between the genera in the bones and the muscles of the wing, tail and hind limb are relatively large. The family may be separated into two groups on the basis of presence or absence of M. caudofemoralis. This muscle is represented in *Coragyps* and *Cathartes* only by the pars caudofemoralis; even this part is absent in *Gymnogyps, Sarcoramphus* and *Vultur*. Garrod (1873:626) did not find M. caudofemoralis in *Sarcoramphus*. Absence of the muscle is not positive proof of close relationship between *Gymnogyps, Vultur* and *Sarcoramphus;* it may have been lost independently in these genera. However, its presence in *Coragyps* and *Cathartes* indicates primitiveness and a similar origin for these forms since it is unlikely that this peculiar muscle would have evolved twice in the history of the vultures.

Similar conclusions regarding their phylogeny were reached in a detailed study of skulls of Recent and fossil cathartids (Fisher, 1944).

Other characters indicate close relationship between *Gymnogyps* and *Vultur*. Both are large, heavy-boned birds, highly specialized for soaring. They have a greater number of secondary and tertiary remiges than do *Coragyps* and *Cathartes;* the humeral feather tracts are identical in the California and Andean condors. *Vultur* and *Gymnogyps* lack eyelashes, but *Cathartes* and *Coragyps* agree in having a single incomplete row on the upper lid and two rows on the lower lid. Placement of feathers in the spinal tract is similar in the condors. As in *Gymnogyps*, the sternal apterium in *Vultur* is enclosed laterally by a single row of feathers; in the black and turkey vultures there are two, and often three, rows of feathers here. In *Cathartes* and *Coragyps* the anal circlet of feathers is incomplete; in *Vultur* and *Gymnogyps* there is at least one complete anal circlet.

Common myological features other than the absence of M. caudofemoralis separate the condors from *Cathartes* and *Coragyps*. The middle third of the tendon of M. tensor patagii longus is elastic in *Vultur* and *Gymnogyps*. *Coragyps* is set off from all the other genera by the absence of a tendon extending posteriorly from the tendon of M. tensor patagii longus toward the elbow. M. latissimus dorsi in the condors has two dermal components; only one is found in *Coragyps*, and *Cathartes* has none. Both the California and Andean condors possess an additional tendon of insertion for M. deltoideus minor. M. subcoracoideus, M. proscapulohumeralis and M. subscapularis are inseparably fused in the condors; only the first two are fused in *Cathartes* and *Coragyps*.

M. adductor profundus is divided into an anterior and a posterior part in *Coragyps;* it is undivided in *Cathartes* and *Vultur* and shows only a partial

division in *Gymnogyps*. In the condors the belly of M. obturator internus has two distinct tendons within it; it is a simple pennate muscle in the small vultures. The inserting tendon of M. flexor perforatus digiti II is not perforated in *Gymnogyps* and *Vultur*.

The characters discussed in the foregoing paragraphs indicate a closer relationship between the two small vultures and among the large condors, including *Sarcoramphus*, than is present between the small vultures and the condors. Certain of these characters tend to show that *Cathartes* and *Coragyps* are of a more primitive stock.

The fossil record of North American Pleistocene, however, shows that *Gymnogyps* was more abundant than *Cathartes* and that *Cathartes* was more plentiful than *Coragyps*. This may indicate that *Gymnogyps* is the earliest of the Recent vultures in North America.

If the cathartids are of South American origin, as Lönnberg (1927:22-23) states, it is possible that the large cathartids, *Teratornis* and *Gymnogyps*, moved into the Nearctic continent with the large mammals of South American origin. The small vultures may have remained in the south because they were unable to compete with the larger cathartids and accipitrids. With the decline of the large mammals and large birds, *Cathartes* may have moved north and may have been followed by *Coragyps*. This perhaps explains the relative abundance of the cathartid genera in the Pleistocene of North America, and if such is the case, *Gymnogyps* is not necessarily the primitive member of the Recent cathartids. The link between the condors and the small vultures should be looked for in the South American fossil beds, and until cathartid material from there is available the phylogeny of the Cathartidae will perhaps remain uncertain.

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DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY,
UNIVERSITY OF HAWAII,
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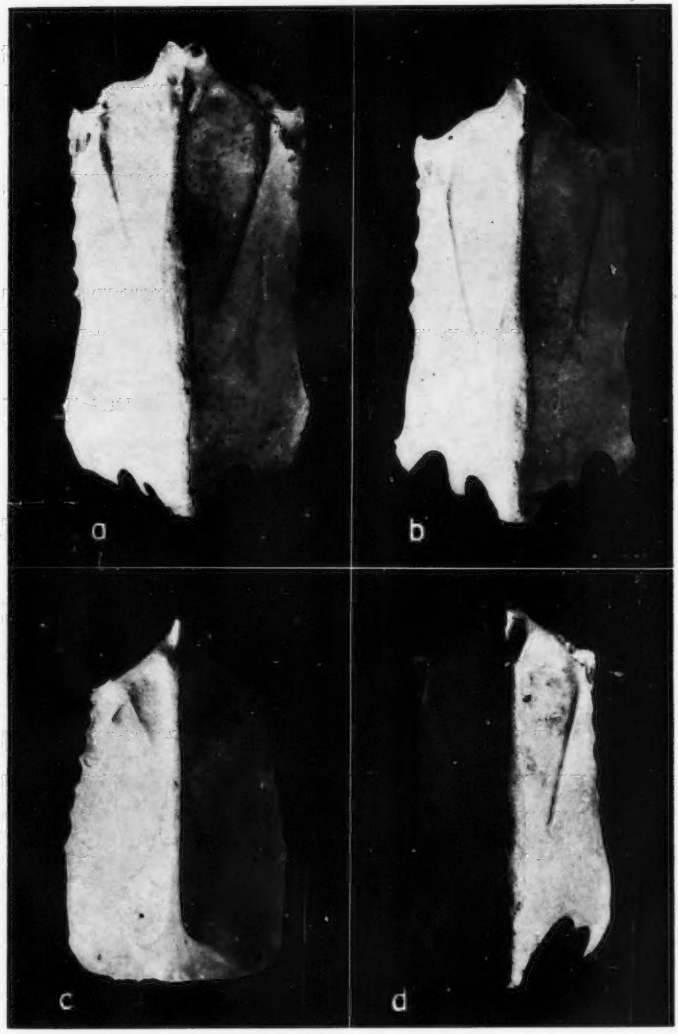

PLATE 1.—Sterna, ventral view. See plate 2. Note difference in shape of carinal apex, ventral manubrial spine, sternocoracoidal process, costal facets, sternal notch, xiphial area and muscle lines and in length and thickness of carina. ×9/20. *a. Vultur gryphus*, no. 1734 coll. Loye Miller. *b. Gymnogyps californianus*, no. 74888 M.V.Z. *c. Aquila chrysaëtos*, no. 74641 M.V.Z. *d. Sarcoramphus papa*, no. 19852 coll. Loye Miller.

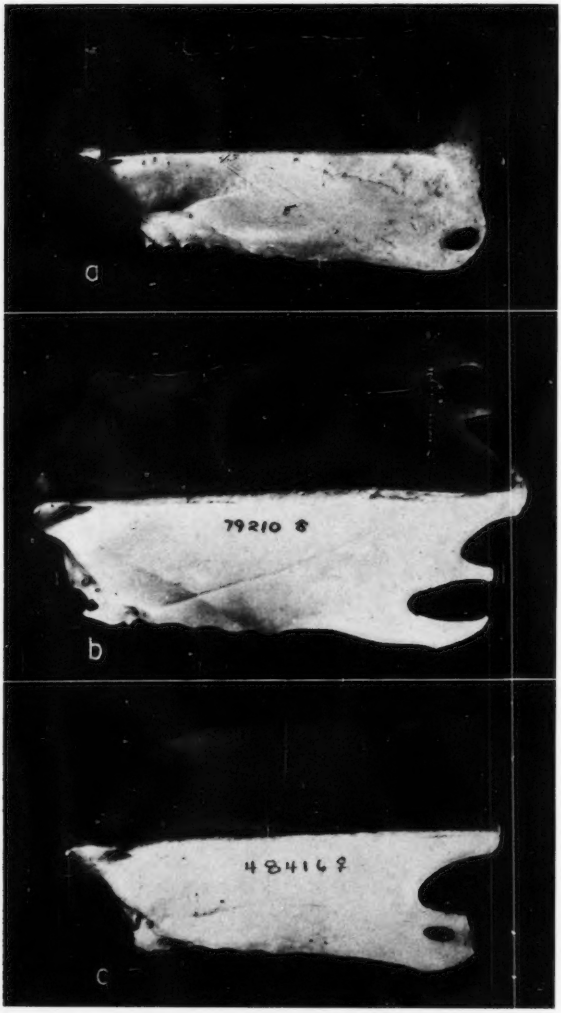

PLATE 2.—Sterna in ventral view, showing differences in shape of carinal apex, width and length of carina, ventral manubrial spine, sternocoracoidal process, costal facets, sternal notch and muscle lines. Note particularly the flaring of lateral parts of the sternal plate and the variation in the xiphial area. ×5/6. *a. Buteo borealis*, no. 54444 M.V.Z. *b. Coragyps atratus*, no. 79210 M.V.Z. *c. Cathartes aura*, no. 48416 M.V.Z.

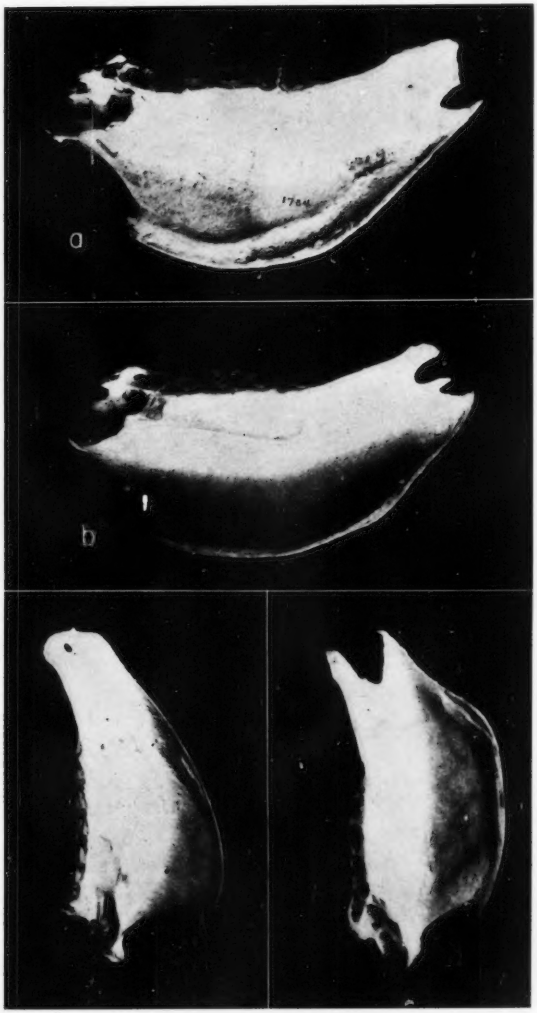

PLATE 3.—Sterna in lateral view, showing differences in pneumaticity, size and shape of ventral manubrial spine, sternocoracoidal process, carinal apex, height and length of carina, shape and direction of muscle lines on carina, number of costal facets, and shape of posterior part of sternal plate. ×2/5. *a. Vultur gryphus*, no. 1734 coll. Loye Miller. *b. Gymnogyps californianus*, no. 74888 M.V.Z. *c. Aquila chrysaëtos*, no. 74641 M.V.Z. *d. Sarcoramphus papa*, no. 19852 coll. Loye Miller.

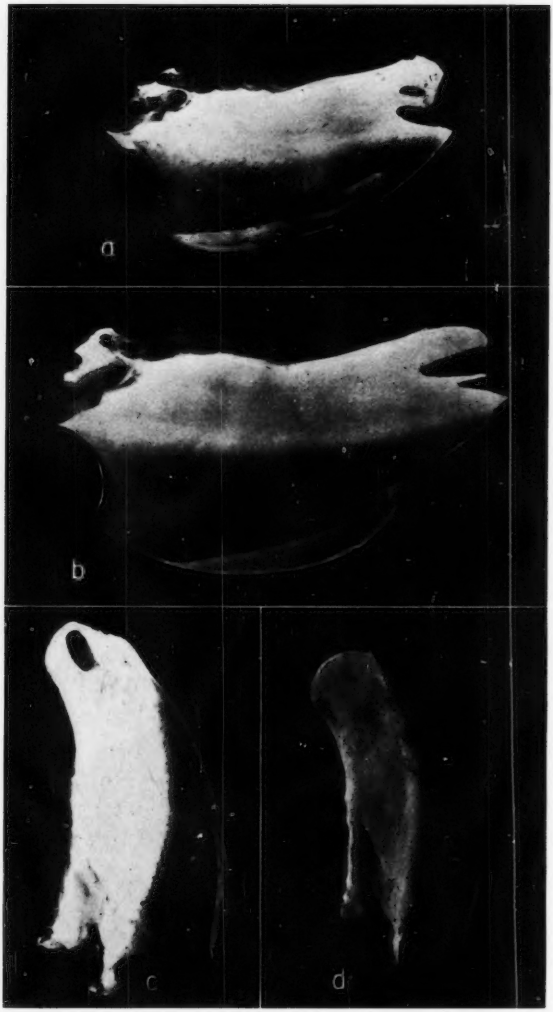

PLATE 4.—Sterna in lateral view. Note variation in size and shape of ventral manubrial spine, sternocoracoidal process, carinal apex, height and length of carina, shape of muscle lines on carina, number of costal facets, and shape of posterior part of sternal plate. ×5/6. *a. Cathartes aura*, no. 48416 M.V.Z. *b. Coragyps atratus*, no. 79210 M.V.Z. *c. Buteo borealis*, no. 54444 M.V.Z. *d. Astur atricapillus*, no. 63058 M.V.Z.

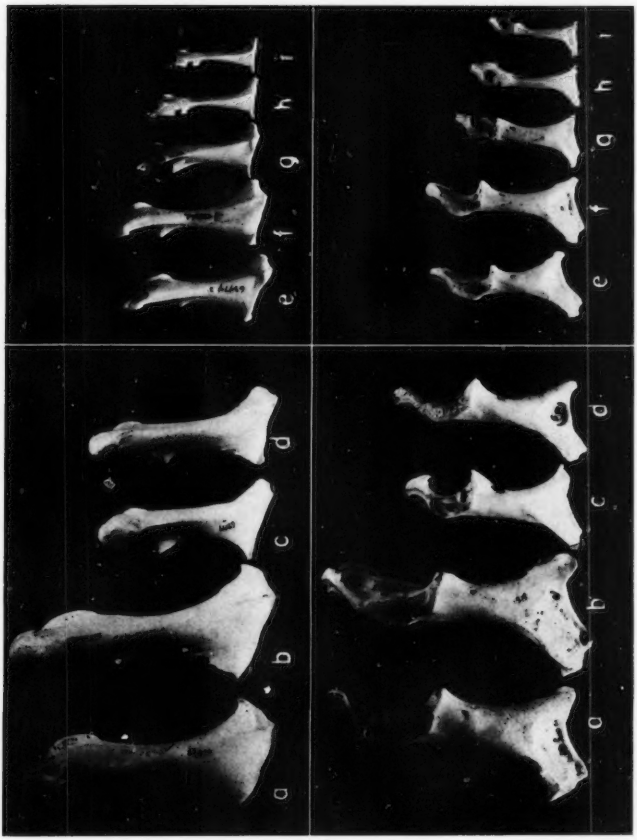

PLATE 5.—Coracoids, anterior and posterior views, showing variation in pneumaticity, development of brachial tuberosity, shape and position of furcular, glenoid and scapular facets, size of triosseal canal, development and location of procoracoid and coracoidal fenestrae, strength of shaft, size of sternocoracoidal process and impression, width of internal distal angle, and the angle the sternal facet makes with the shaft. All ×3/8. *a. Gymnogyps californianus*, no. 74888 M.V.Z. *b. Vultur gryphus*, no. 218 coll. Loye Miller. *c. Aquila chrysaëtos*, no. 63177 M.V.Z. *d. Sarcoramphus papa*, no. 686 coll. Loye Miller. *e. Cathartes aura*, no. 63474 M.V.Z. *f. Coragyps atratus*, no. 79210 M.V.Z. *g. Buteo borealis*, no. 54444 M.V.Z. *h. Astur atricapillus*, no. 71809 M.V.Z. *i. Accipiter cooperii*, no. 74933 M.V.Z.

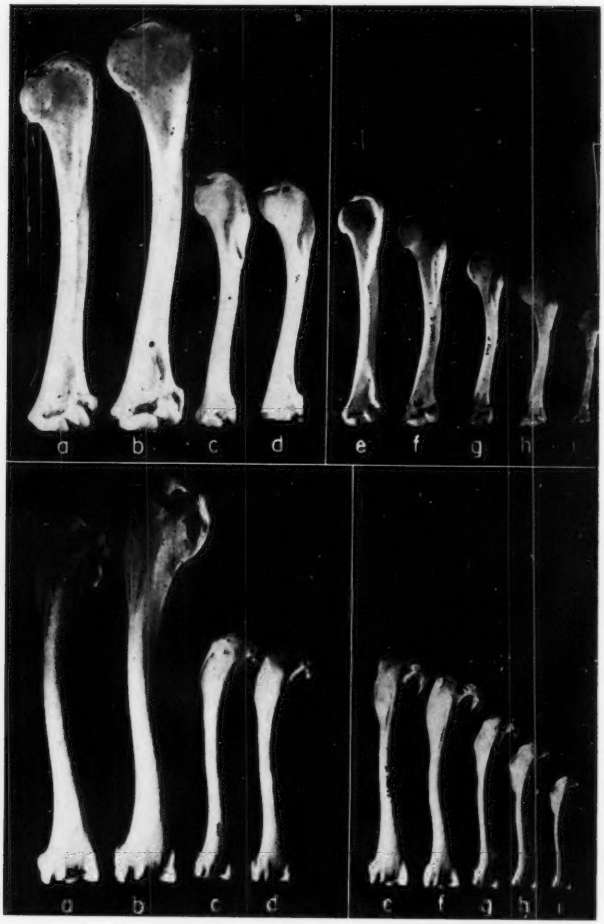

PLATE 6.—Humeri, palmar and anconal views. Note differences in pneumaticity, position and shape of deltoid and bicipital crests, development of external tuberosity, angle of median crest, depth of capital groove, curvature of shaft, width and depth of brachial depression, development of condyles and the entepicondyle, and depth of the oleocranal fossa. All ×2/9. *a. Gymnogyps californianus*, no. 74888 M.V.Z. *b. Vultur gryphus*, no. 1734 coll. Loye Miller. *c. Aquila chrysaëtos*, no. 63177 M.V.Z. *d. Sarcoramphus papa*, no. 686 coll. Loye Miller. *e. Cathartes aura*, no. 63474 M.V.Z. *f. Coragyps atratus*, no. 79209 M.V.Z. *g. Buteo borealis*, no. 41229 M.V.Z. *h. Astur atricapillus*, no. 63058 M.V.Z. *i. Accipiter cooperii*, no. 74933 M.V.Z.

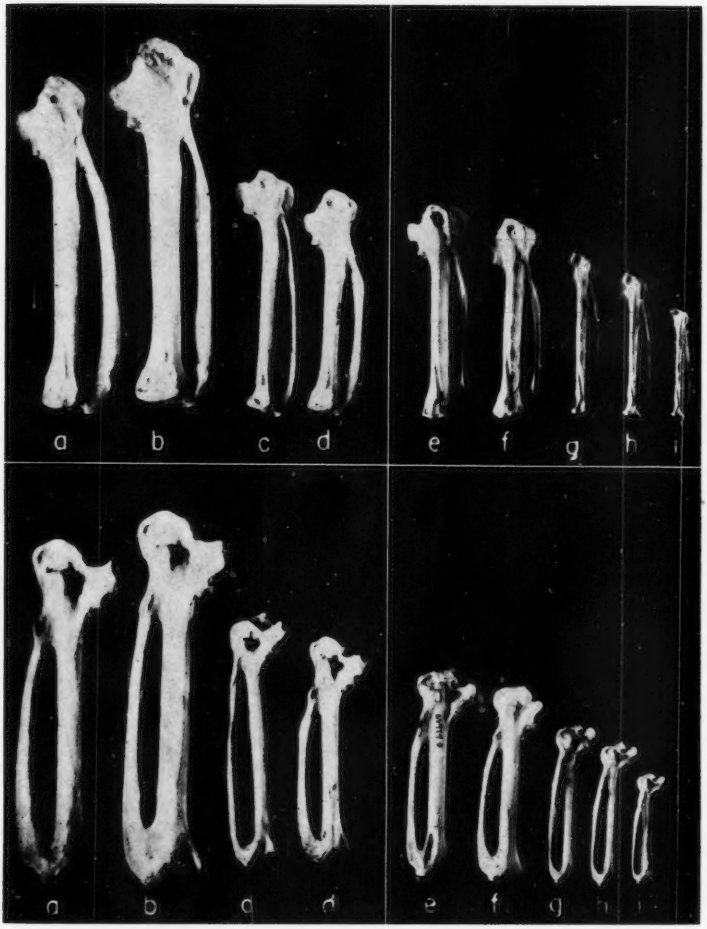

PLATE 7.—Metacarpi, palmar and anconal views. Observe variation in the placement and direction of metacarpal I and the pollical facet, depth of the anterior carpal fossa, slope of the carpal trochlea, sturdiness of metacarpal III, size and shape of flexor attachments on metacarpals II and III, position of tendinal groove on metacarpal II, width and length of intermetacarpal space, and shape and position of facets for digits II and III. All 3/8. *a. Gymnogyps californianus*, no. 74888 M.V.Z. *b. Vultur gryphus*, no. 1734 coll. Loye Miller. *c. Aquila chrysaëtos*, no. 63177 M.V.Z. *d. Sarcoramphus papa*, no. 19852 coll. Loye Miller. *e. Cathartes aura*, no. 63474 M.V.Z. *f. Coragyps atratus*, no. 79209 M.V.Z. *g. Buteo borealis*, no. 41229 M.V.Z. *h. Astur atricapillus*, no. 63058 M.V.Z. *i. Accipiter cooperii*, no. 74933 M.V.Z.

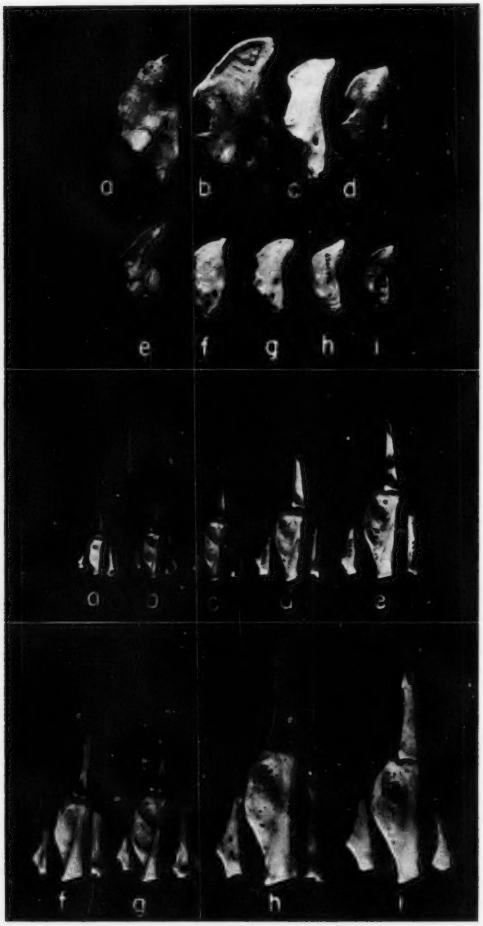

PLATE 8.—Pygostyles, lateral view, showing differences in extent and in shape of crest. All ×9/20. *a. Gymnogyps californianus*, no. 386 coll. Loye Miller. *b. Vultur gryphus*, no 1734 coll. Loye Miller. *c. Aquila chrysaëtos*, no. 74641 M.V.Z. *d. Sarcoramphus papa*, no. 686 coll. Loye Miller. *e. Cathartes aura*, no. 48416 M.V.Z. *f. Coragyps atratus*, no. 79210 M.V.Z. *g. Buteo borealis*, no. 54444 M.V.Z. *h. Astur atricapillus*, no. 63058 M.V.Z. *i. Accipiter cooperii*, no. 62395 M.V.Z.

Digits of the wing. Note differences in relative lengths of parts and in pneumaticity. All ×1/3. *a. Accipiter cooperii*, no. 74933 M.V.Z. *b. Astur atricapillus*, no. 63058 M.V.Z. *c. Buteo borealis*, no. 54444 M.V.Z. *d. Coragyps atratus*, no. 79210 M.V.Z. *e. Cathartes aura*, no. 48416 M.V.Z. *f. Sarcoramphus papa*, no. 686 coll. Loye Miller. *g. Aquila chrysaëtos*, no. 61231 M.V.Z. *h. Vultur gryphus*, no. 1734 coll. Loye Miller. *i. Gymnogyps californianus*, no. 74888 M.V.Z.

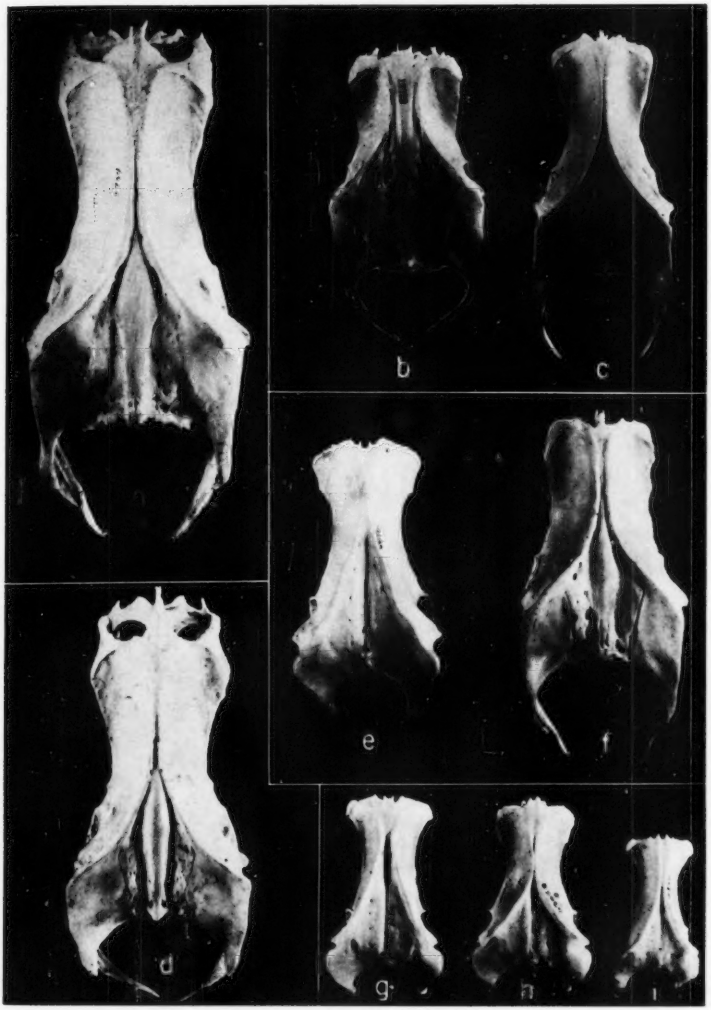

PLATE 9.—Synsacra, dorsal view, showing differences in relative width, in development of ilial fossa, in degree of fusion of sacral vertebrae and in extent of postacetabular region. All ×9/20. *a. Vultur gryphus*, no. 1734 coll. Loye Miller. *b. Cathartes aura*, no. 12713 M.V.Z. *c. Coragyps atratus*, no. 79210 M.V.Z. *d. Gymnogyps californianus*, no. 386 coll. Loye Miller. *e. Aquila chrysaëtos*, no. 63177 M.V.Z. *f. Sarcoramphus papa*, no. 19852 coll. Loye Miller. *g. Buteo borealis*, no. 41229 M.V.Z. *h. Astur atricapillus*, no. 63058 M.V.Z. *i. Accipiter cooperii*, no. 74933 M.V.Z.

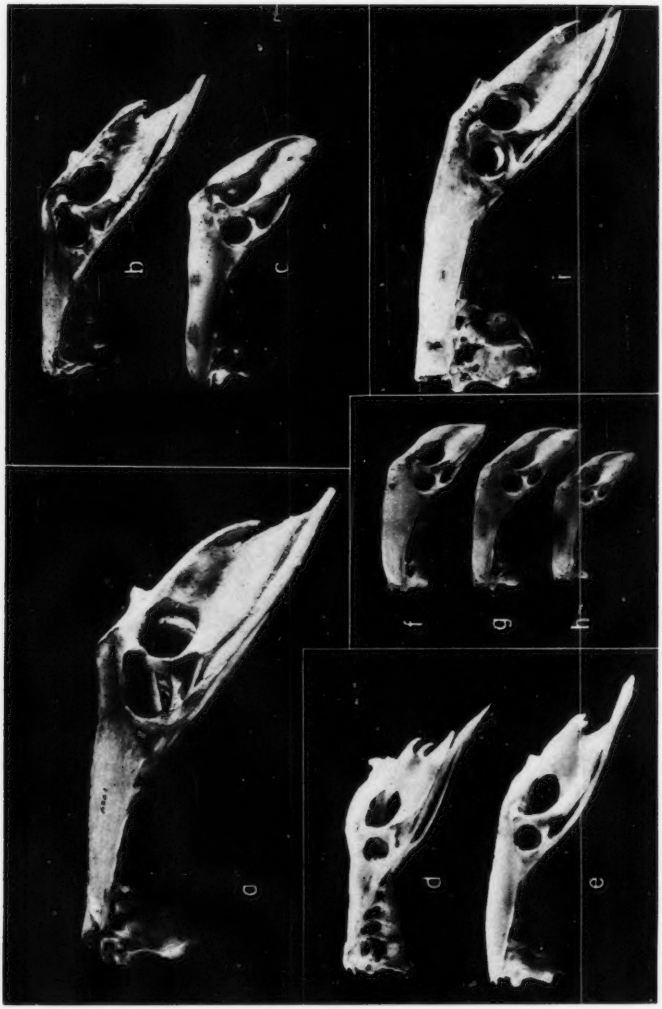

PLATE 10.—Synsacra, lateral view, showing differences in depth, in angle of pre- and postacetabular regions and in development of pubis and ischium. All ×2/5. *a. Vultur gryphus*, no. 1734 coll. Loye Miller. *b. Sarcoramphus papa*, no. 19852 coll. Loye Miller. *c. Aquila chrysaëtos*, no. 63177 M.V.Z. *d. Cathartes aura*, no. 12713 M.V.Z. *e. Coragyps atratus*, no. 79210 M.V.Z. *f. Buteo borealis*, no. 41229 M.V.Z. *g. Astur atricapillus*, no. 63058 M.V.Z. *h. Accipiter cooperii*, no. 74933 M.V.Z. *i. Gymnogyps californianus*, no. 386 coll. Loye Miller.

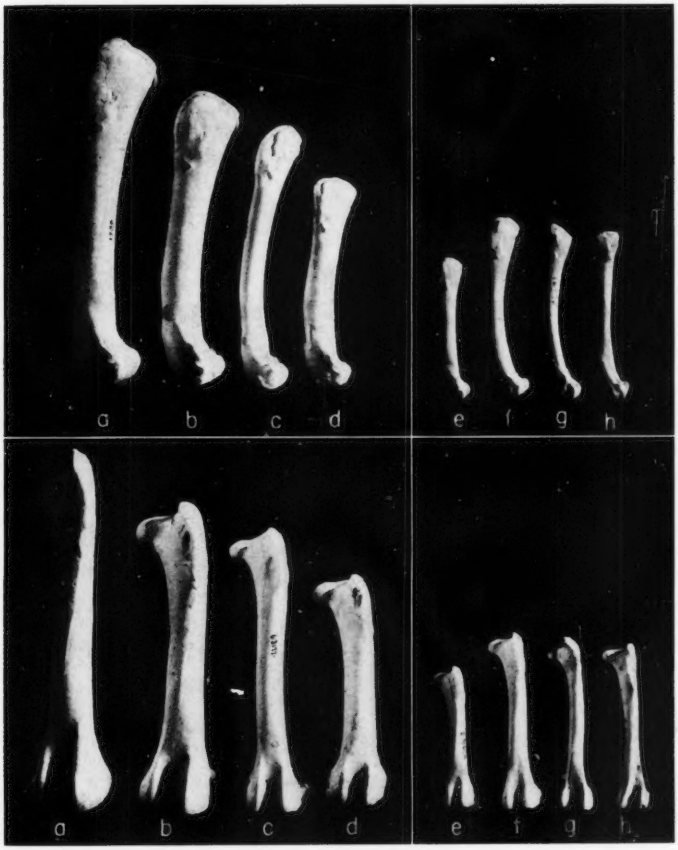

PLATE 11.—Femora, anterior and lateral views, showing differences in head and neck, in attachments of muscles on trochanter, in degree of curvature of shaft, in pneumaticity, and in width, medial displacement and direction of rotular groove. All ×1/3. *a. Vultur gryphus*, no. 1734 coll. Loye Miller. *b. Gymnogyps californianus*, no. 74888 M.V.Z. *c. Aquila chrysaëtos*, no. 63177 M.V.Z. *d. Sarcoramphus papa*, no. 19852 coll. Loye Miller. *e. Cathartes aura*, no. 63474 M.V.Z. *f. Coragyps atratus*, no. 79210 M.V.Z. *g. Gallus domesticus*, no. 12495 M.V.Z. *h. Pandion haliaëtus*, no. 63066 M.V.Z.

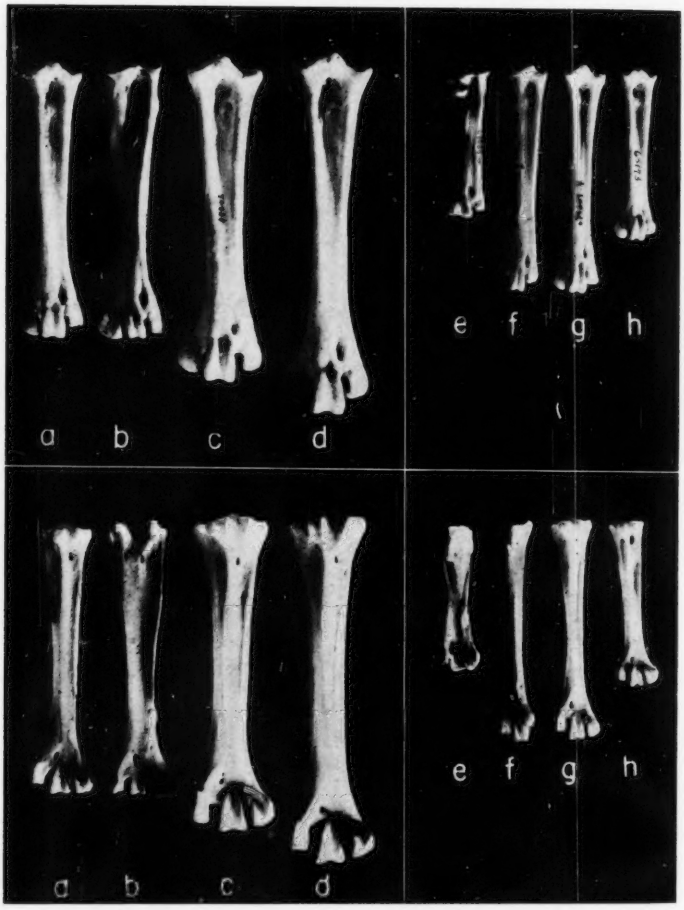

PLATE 12.—Tarsometatarsi, anterior and posterior views, showing differences in shape of head, in development of hypotarsus, in anterior and posterior muscular grooves and in shape and position of trochlea. All ×9/20. *a. Sarcoramphus papa*, no. 19852 coll. Loye Miller. *b. Aquila chrysaëtos*, no. 63177 M.V.Z. *c. Gymnogyps californianus*, no. 74888 M.V.Z. *d. Vultur gryphus*, no. 218 coll. Loye Miller. *e. Pandion haliaëtus*, no. 63066 M.V.Z. *f. Gallus domesticus*, no. 12495 M.V.Z. *g. Coragyps atratus*, no. 79209 M.V.Z. *h. Cathartes aura*, no. 65173 M.V.Z.

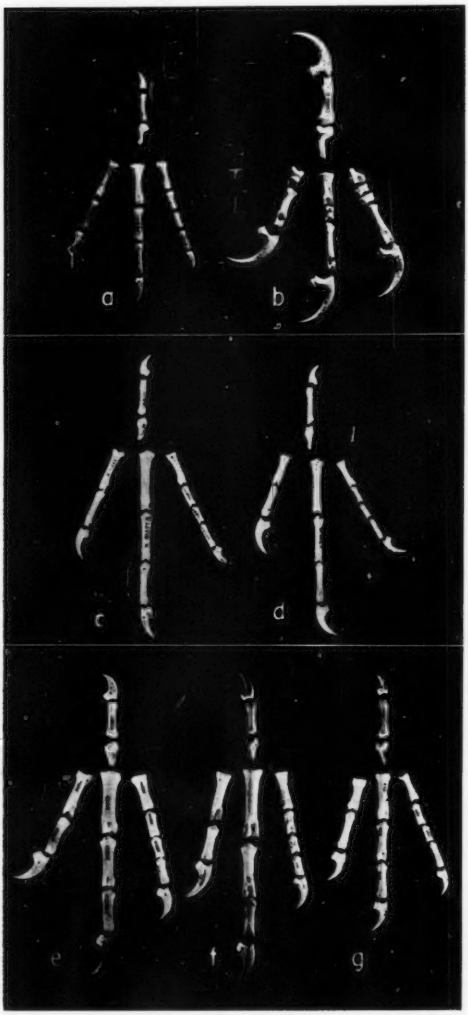

PLATE 13.—Bones of foot, dorsal view, showing differences in length and strength of phalanges. Note differences in length and curvature of the claws. a.—d. ×1/3, e.—g. ×1/4. *a. Gallus domesticus*, no. 12495 M.V.Z. *b. Pandion haliaëtus*, no. 63066 M.V.Z. *c. Coragyps atratus*, no. 79210 M.V.Z. *d. Cathartes aura*, no. 63475 M.V.Z. *e. Gymnogyps californianus*, no. 74888 M.V.Z. *f. Vultur gryphus*, no. 218 coll. Loye Miller. *g. Sarcoramphus papa*, no. 686 coll. Loye Miller.

Observations on the Life History of the Horned Passalus

I. E. Gray

Introduction

The horned passalus, *Popilius disjunctus* Illiger,* is an interesting social beetle that lives in rotting hardwood logs. It has a wide distribution in the United States and is especially abundant in the Southern states where adults may be taken at all seasons of the year. The shiny black integument has given it the common name of "patent leather beetle." In some localities it is also known as the Betsy beetle. The majority of approximately five hundred species of beetles belonging to the family Passalidae are tropical and occur in both the old world and the new, but *Popilius disjunctus* is the only common member of the family to be found in this country.

Because of its ready availability, its large size, and its interesting habits this beetle has been used extensively for research, but in spite of this there are numerous gaps in our knowledge of its life history, habits, and ecology. Observations by Ohaus (1900, 1909) on South American species and studies by Gravely (1914-1916) on Indian and Oriental passalids have added much to our knowledge of the life history and habits of passalids in general, but not of *P. disjunctus*, in particular. In the literature most of the generalizations about passalids are based on South American species as observed by Ohaus.

Riley (1872, 1873) found the eggs of passalus and called attention to the surprisingly brief period of larval development. Hinds (1901) tested the strength of passalus under various conditions and tried in vain to find external morphological differences in sex. Babb (1901) described the method of stridulation in adults. Ohaus (1900, 1909) made extensive studies of the social behavior and life histories of several species of passalids from Brazil. The Brazilian passalids apparently have more in common with *P. disjunctus* than do the numerous oriental species studied by Gravely (1914-1916). Wheeler (1923) showed the position of passalus in the evolution of social life among insects. Miller (1931) devised a method by which pupal case building could be observed in the laboratory. Parks (1935, 1937) included passalus in his studies of rhythmicity in insects. Pearse (1936) added to our knowledge of the ecology of passalus, especially with reference to food habits and parasites. Gray (1944) followed the changes in water content throughout the life cycle from egg to adult. Other authors (Patterson 1937, Krause 1943, Cody and Gray 1938) have studied various phases of anatomy and reproduction.

In view of the frequent use made of passalus as a research animal, it seems worthwhile to bring together what is already known of its life history with such additional information as has accumulated from several years of study of this interesting beetle.

* *Passalus cornutus* Fabricius of many authors.

Grateful acknowledgement is made to Mrs. Frances McNabb, Mr. James Mangrum, and Dr. James Starling, who at one time or another have assisted in the collection, care, and study of passalus.

Adults

It is well known that passalid beetles make extensive tunnels in hardwood logs. In the Duke Forest, where many thousands have been taken, *Popilius disjunctus* has been found repeatedly in rotting logs and stumps of nearly all species of trees except pine and cedar. On very rare occasions a few have been found in pine, but none has ever been taken from cedar. Pearse (1936) states that passalus prefers oak, but it seems to be equally abundant in hickory, gum, and poplar. It occurs somewhat less frequently in dogwood. The availability of the logs and the degree of decomposition seem to be more important factors than the species of hardwood.

Adults have occasionally been found outside of the tunnels. They have been taken on highways and near dwellings that are not far from wooded areas. On early morning field trips, particularly in the spring, they have been found near logs that show evidence of having been chewed by the beetles in an effort to gain entrance. Probably entrance into new logs is ordinarily made at night and those few stragglers found outside the logs were caught by daylight before the tunnel was well started. What means of transportation, other than crawling, that the adults use when outside of the logs could not be determined. No way has been found to make them use their wings. Tossing in the air and dropping from tall buildings, even with elytra unhooked and wings expanded for them, have brought negative results. The suspicion is strong that the wings are never used for anything but stridulation. In fact, it is doubtful if passalus can even unhook the elytra. This is not surprising, for several members of the Passalidae have fused wing-covers. Under normal conditions passalids have little use for wings as organs of flight.

There is evidence for believing that the adults do not always choose wisely in selecting logs for their tunnels. Several times dead beetles have been recovered from newly made tunnels just under the bark of logs exposed to bright sunlight. On one occasion, in late May, two dead adults were found under the bark in a small freshly made tunnel that contained two newly laid eggs. For a week the weather had been cool and rainy or cloudy. The day before the beetles were found the sun came out unusually hot. The log was in a position to be exposed to the hot rays of the sun for five or six hours. Undoubtedly the excessive heat created within the tunnel caused the death of the beetles. Savely (1939) has shown that the temperature under the bark of logs exposed to direct sunlight may be as much as eleven degrees higher than the temperature outside the log. Passalus seems quite frequently to be caught in such fatal circumstances. Sometimes, however, under favorable weather conditions, passalus can make use of large logs exposed to bright sunlight, although those in more moist situations are undoubtedly preferred. In early spring tunnels under the bark on the upper side may be inhabited even though the log is in the sun, but as the season progresses and the maximum temperature rises, the tunnels

are extended deeper into the logs and to the under side where the beetles are not adversely affected by the sun's rays.

The length and ramifications of the tunnels are variable. In fallen tree limbs of small diameter there may be but a single tunnel with few or no side excavations; in large logs there may be many colonies of beetles and the ramifications of the tunnels may be extensive and communicate with those of other colonies. In general the tunnels follow the grain of the wood. It is not unusual to find tunnels as much as ten feet long. The great extensions to the galleries are made during the summer months when living space has to be considerably enlarged to make room for the young and food must be prepared to feed them. Eggs seem always to be laid in newly-made galleries, well stocked with triturated food prepared by the adults.

Passalus beetles are not as gregarious during the egg-laying season, when new colonies are getting started, as they are at other seasons. Seldom is more than one pair, male and female, to be found in the same gallery during late spring and early summer, when eggs are being laid and larvae are being cared for. In fact, the addition of a third beetle is resented and a fight ensues with much clashing of mandibles and loud stridulations. Galleries of one colony do not connect with the galleries of another colony in the same log until late in the summer, but after the new generation of adults begins to appear it is not uncommon for the members of several colonies to mingle. At this time the runways may become crowded with beetles of both sexes. These are both old adults and new. Pearse (1936) says that "as many as ninety-odd passali were found in one large log. These were members of several colonies." He makes no mention of the season of year when this many were found, but ninety would not by any means be an excessive number for one large log in late August or September. The sex ratio is 1:1 throughout the year.

After making many attempts without success to determine a sexual dimorphism one is forced to agree with Hinds (1901) that there seems to be no infallible rule for easily distinguishing males from females. By lifting the wing covers and exerting slight pressure on the abdominal segments the genitalia may be caused to be extruded. The edeagus of the male is readily forced out in this manner. This method of telling males from females, however, is unsatisfactory for experimental animals, for even slight ruptures sometimes prove fatal to the beetles. On the average females are larger and weigh twelve per cent more than males. Data on some one thousand beetles show that males range in length from 26.5 mm. to 35.0 mm. (average, 31.5 mm.) and average about 1,480 mg. in weight, while females range from 28.5 mm. to 37.0 mm. in length (average, 33.0 mm.) and weigh on the average approximately 1,685 mg. Measurements of the length of adults were made by micrometer calipers from posterior end of the elytra to the distal end of the horn on the head. Passalus is a prognathus beetle and the mandibles protrude beyond the end of the horn, but as the jaws are movable, measurement to the end of the mandibles gave inconsistent measurements. Usually the very smallest beetles are males and the very largest females, but there are exceptions to this and beetles of average size may be either male or female. This overlapping in size is shown in Figure 3. In spring and early summer, when the adults are in pairs,

usually the larger of the two is the female, but here again there are exceptions.

The length of life of passalus is not known but presumably it is several years. It is known that they live at least two years and there are indications that they may live longer than that. A number that were at least a year old were liberated after being marked by making incisions through the integument of the prothorax. Some were recovered a year later with the wounds scarcely visible and a few were recovered two years later in the same log where marked beetles were liberated, but the identification marks were so indistinct that we were not positive that they were the same specimens liberated two years before.

The number of years that a log is habitable by passalus is variable and evidently depends on moisture conditions and whether the wood is suitable for food. Savely (1939) has found passalus in logs only two years old. The species is abundant in logs three, four, and five or more years old. One large oak log some three feet in diameter in the Duke Forest has served as a source of beetles for over ten years. Passalus has difficulty in tunneling until the log begins to rot. Within logs the adults avoid the harder parts and follow the rotting areas.

Two sizes of wood pulp are produced. When starting a new gallery or when it becomes necessary to enlarge a tunnel very rapidly, the wood chips are quite large. Sometimes the pieces are as large as a dime. Often these are removed from the galleries and piled outside the log at the entrance. The pulp used as food for the young, however, is of fine texture and is packed along the floor and walls of the galleries.

It has been assumed, on the basis that some have been found outside of logs on dark days and early in the morning, that passalus was primarily a nocturnal animal. However, Park (1937) has shown the adults to be arhythmic. Under constant environmental conditions activity was found to be equally distributed over the twenty-four hour period. Park made no study of the larvae, but casual observations in the laboratory indicate that these, too, show no periodicity of activity.

In the Piedmont region of North Carolina adults are readily available in any month of the year. During periods of cold weather, as during periods of hot weather, they usually crawl deep within the log or seek the under side, where temperature conditions are more stable than just under the bark. In sections of the country where the winters are more rigorous undoubtedly passalus hibernates during the coldest weather. Blatchley (1910) gives the collecting dates in Indiana as January 11 to November 26.

Life Cycle

The cycle from egg to imago is completed in two and one half to three months, a rather short time for so large a beetle. There is but one generation per year and the developmental stages may be found only during a limited period in the summer season. In the vicinity of Durham, N. C., most egg-laying is accomplished during the month of June. Newly laid eggs, however, have been taken as early as May 15 and, in a few scattered cases, as late as the first week in August. In the natural galleries eggs are always laid in the midst of the finely chewed decayed wood that has been previously prepared

by the adults. Although all eggs of one female are kept in one egg-nest in the gallery, they are not all laid at the same time. Egg-laying for each female evidently continues over a period of two or more weeks. Evidences from dissections in the laboratory and from observations in the field indicate that under normal conditions two eggs are laid at one time. In dissections of females freshly brought in from the woods during the egg-laying period never more than two ripe eggs were found in the reproductive ducts. These were always bright red in color, as are the newly laid eggs in the galleries. In the laboratory females have been known to lay as many as six eggs in twenty-four hours, but usually only two or four eggs were laid during this period. Evidently females brought to the laboratory sometimes hold their eggs in the uterus for a day or two before laying them. Since adults have occasionally been observed carrying eggs in their mandibles, it is thought that eggs are laid anywhere in the galleries but are carried by the adults to the single egg nest. In the laboratory at 27° C. the eggs hatch in about 16 days.

The number of eggs to be found in an egg nest varies, but usually there are between 20 and 35 when all have been laid. Sixty eggs is the largest number found in any one batch. In another case thirty-eight eggs and thirteen first instar larvae were found. As the eggs are not all laid at the same time there is a big difference in time of hatching. Often many eggs have hatched before the female has completed ovipositing. In fact, it is not unusual for some of the larvae to be in the second instar while eggs are still being laid. This leads to a great variation in the size of the larvae in the same colony. It was this condition that led Riley (1872) to conclude erroneously that passalus spent two years in the larval stage; for with the finding of both large and small larvae in the same colony, he quite naturally assumed that the largest were from eggs of the previous year. Riley (1873) discovered his error the following year and was astonished to find that the life cycle could be completed in one season.

There are three larval instars. First instar larvae are abundant throughout the month of June, particularly in the last half of the month, and during the first half of July. Second instar larvae are abundant during the last half of June and throughout July. July and most of August is the most favorable time to collect third instar larvae. In the laboratory at 27° C. 12 to 18 days are spent in the first instar, 10-15 days in the second instar, and 25 or more days in the third instar. Larvae are white on hatching but within twenty-four hours, as soon as feeding is well underway, they take on their characteristic bluish color which is maintained until the prepupal stage. There is a short prepupal stage of about five days when the third instar larvae cease feeding, lose their blue color, assume a fatty appearance, and wander about seeking a place in which to pupate. In the laboratory without the presence of adults, the prepupae when about to pupate burrow in the moist wood pulp or hollow out a place on the surface. This hollowing out process is done by frequently rolling over and over. Under natural conditions in logs a cocoon of mud or wood pulp is built around the prepupa by the adults.

The pupal stage at 27° C. lasts 10 to 12 days. Early pupae are white but in later stages they take on a pinkish tint here and there, particularly in the prothorax. A day or two before metamorphosis is completed the reddish color

of the prothorax and underparts becomes quite pronounced. From the intensity of this color the length of time before the adults will emerge can be estimated quite accurately. When it first emerges from its pupal skin the newly formed adult, with its white elytra and red head and prothorax, makes a very striking appearance. In a few hours the elytra assume a pinkish tint and finally become red like the rest of the beetle. New adults remain in their pupal cases for several days after metamorphosis is completed. Sclerotization in passalus takes place slowly and for several days after transformation the integument remains quite soft. Were they to enter the runways in this condition they would be subject to the attacks of other members of the colony.

The red color of the new adults last a varying length of time. The beetles gradually become darker, taking on a reddish-black appearance before finally becoming entirely black. Some become black in a few weeks; others not for several months. The red adults are not sexually mature and a new generation is not produced until the following summer.

The approximate time required for passalus to complete its cycle is shown in Figure 1. Probably the cycle is completed in somewhat shorter time in the natural galleries than in the laboratory at 27° C. Figure 2 shows the months when the different stages are abundant in the Duke Forest.

Eggs

Probably the first to observe passalus eggs was Riley (1873), who noted that "the shell is smooth, flexible, but tough, and of various shades of olive-green, yellow, or brown." Riley did not study the development of the eggs and

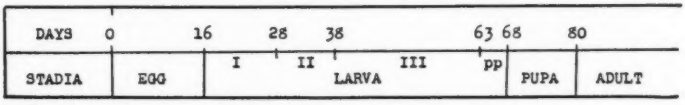

Fig. 1.—Typical developmental timetable for *Popilius disjunctus*. I, II, III, the three larval instars; pp, prepupa.

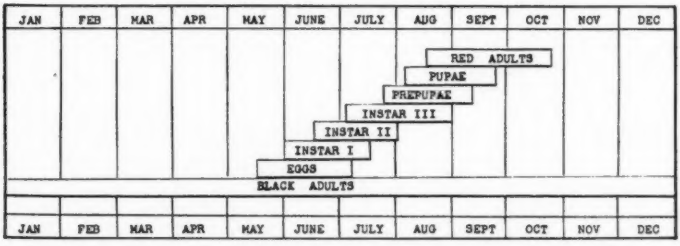

Fig. 2.—The most favorable times for collecting the various developmental stages of *Popilius disjunctus*. Adults are available at all seasons of the year; other stages may sometimes be found outside the ranges given but not in sufficient numbers to make collecting them worthwhile.

consequently saw no significance in the different colors. There is, however, a more or less orderly sequence of color change as the egg develops. Eggs, when first laid, are bright red in color. This gradually changes to a reddish brown during the first week, then to a brownish green, and finally to a dark green. The dark green eggs are within a very few days of hatching. What causes the color changes is not known, but correlated with them are changes in size, weight, and water content. Newly laid eggs are ovoid in shape, with the anterior end slightly larger than the posterior end, and measure about 3.2 mm. by 2.4 mm. At time of hatching the average size has increased to 3.7 mm. by 3.2 mm. The average weight of the egg increases from 10.9 mg. to 19.8 mg. In a previous paper (Gray, 1944), it was shown that the increase in weight and volume are brought about by absorption of water. The water content of a newly laid egg is about 68 per cent; of an egg ready to hatch, about 83 per cent. Eggs, even from the same female, are by no means uniform in size and weight at any particular age. The eggs of *P. disjunctus*, although large as insect eggs go, are dwarfed in size by the eggs of some of the South American passalids, which Ohaus describes as being as much as 5 mm. in length. *P. disjunctus*, however, apparently lays a much larger number.

Until late in development the eggs are tough and flexible and bounce when dropped on a hard surface. However, a day or two before hatching the shell becomes noticeably thinner. At this time the egg is obviously under considerable tension and ruptures easily. At time of eclosion of the larva the egg shell splits lengthwise from one end to the other along the back of the young larva. Usually it is only a minute or two before the larva is free, but occasionally some little time elapses before the head, which is the last part to be withdrawn, can be freed from the shell.

Large numbers of eggs of known age are obtained only with difficulty, for each female lays only a few at a time and probably the total number laid by any one female seldom reaches sixty. To obtain eggs of known age large numbers of beetles were brought in from the woods during the laying season. Each was placed in a separate finger bowl with a half-inch layer of moist wood pulp from the tunnels. The finger bowls were then stacked in a darkened cabinet kept at approximately 27° C. The dishes were examined each day for bright red eggs, which were removed and placed on moist filter paper or moist wood pulp in petri dishes. As far as could be determined, if sufficient moisture was supplied, eggs laid in the laboratory developed as normally as those brought in from the forest.

As many as sixty or seventy eggs can be obtained daily from a hundred female beetles during the height of the laying season, but it was found necessary to replenish the supply of egg-laying females every few days, for after a week or so in finger bowls they either ceased laying entirely, or laid greenish eggs that were subnormal in size. Females may be induced to lay eggs in finger bowls containing nothing but moist filter paper, but under this condition the adult will sometimes carry an egg around in her mandibles for a long time, evidently seeking the proper environment in which to deposit it. Even vigorous shaking will not induce the beetle to drop the egg.

Larvae

Passalus larvae are easily identified in the logs by the blue color and modified third pair of legs. That there are three larval instars was clearly established by application of Dyar's Law and confirmed by direct observation. Dyar (1890), after studying the moulting of caterpillars, proposed the principle that the sclerotized parts of the exoskeleton do not change between moults. This principle has been employed in determining the number of moults of larvae under conditions where the process of moulting cannot be easily observed or where the exuvii cannot be readily recovered. In passalus the old larval skin is easily lost in the wood pulp and is often eaten by the larvae so that the application of Dyar's Law was especially helpful. Data obtained from measurements of the headwidths of over a thousand larvae, made with vernier callipers to the nearest tenth millimeter, clearly indicate that Dyar's Law applies in the case of passalus. These data are summarized in Table 1 and Figure 3 where it may be easily seen that the larvae fall into three distinct groups with no overlapping of the different instars in head-widths. The larger first instar larvae just before moulting often are longer than the smaller second instar larvae just after moulting. The overlapping in length between second and third instars is quite marked, about 30 per cent, and of course this makes it dangerous to estimate the instar by length alone. But the head-widths of the different instars are so distinct that one quickly learns to pick out the different instars by this means without making measurements.

TABLE 1.—Head width and total length of Passalus at different ages. Based on measurements of over 1600 larvae and 1000 adults.

Stadium	Total length mm.	Head width mm.
1st Instar	8.5-20.3	2.0-2.6
2nd Instar	18.5-32.0	3.0-3.7
3rd Instar	26.2-43.0	4.7-5.7
Prepupae	38.0-43.0	4.7-5.7
Pupae & Adults		
Male	26.5-35.0	6.9-8.4
Female	28.5-37.0	7.4-9.1

At time of hatching from the egg passalus larvae vary in length from 8.5 mm. to 11.5 mm., and are white in color. After beginning to feed the larvae take on a bluish color, apparently due to the food in the intestine. This blue tint is characteristic of the larvae of all instars up to the prepupal period. First instar larvae are unable to eat wood that is not already prepared for them by the adults, but feed voraciously and are easily reared on triturated wood pulp brought in from the woods. In the natural logs the newly hatched larvae remain close to the egg nest, but as they become older they extend their wanderings in the tunnels. By the time the third instar is reached members of the same colony may have dispersed to the limits of their living quarters. No feeding time is lost in moulting. Larvae feed right up to moulting time, moult and go on feeding again. The shedding of the larval exuvii takes only a few minutes.

Passalus grubs, like most insect larvae, are voracious feeders. The food consists of rotting wood pulp triturated by the adults. The adults are extremely active, extending the tunnels as the larvae grow and lining the galleries with the finely chewed pulp. This previously prepared food seems to be the principal, if not the only, source of food for the larvae. First instar larvae are unable to chew unprepared pieces of wood. Second and third instar larvae, especially the latter, are physically capable of biting into rotting wood and in the laboratory have been observed doing it, but it is very doubtful if they could get

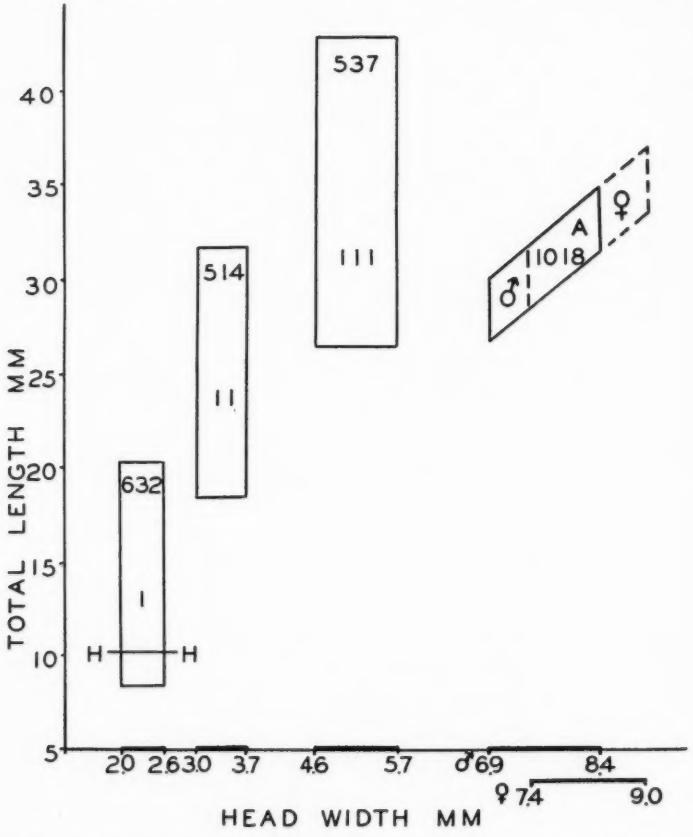

Fig. 3.—Head width and total length of larval and adult passalus. I, II, III, the three larval instars; A, adult; H-H, average length at hatching. The figures refer to the number of individuals measured. Adult males are in solid lines, adult females in dotted lines. The head widths of the different larval instars are distinct, but in adults there is a general correlation between head widths and total lengths.

enough nourishment from it to complete their growth and development without supplementing it with prepared pulp.

Larvae are not difficult to raise in the laboratory if kept supplied with a sufficient quantity of moist pulp from the natural galleries. From 10 to 20 second or third instar larvae may be reared in a large (10 to 12 inch) covered finger bowl in which there is food to a depth of an inch or more. Single isolated larvae do not seem to thrive as well as do those in colonies of several. Small first instar larvae should be isolated from the larger larvae, for they are very easily injured. Once the integument is punctured there is little hope of recovery. Injured and weak larvae are usually eaten by the others. In the laboratory the larvae thrive better without adults, for it all too frequently happens that the adults turn cannibalistic and kill the larvae.

To be used as food the triturated pulp must be kept moist. If not, seemingly the larvae can make no use of it. Larvae do not occur in dry logs. The moisture content of the pulp from the natural galleries has been determined on several occasions and in each case was found to be about 85 per cent.

In a series of feeding experiments with third instar larvae in which each larva was kept in a covered finger bowl with a known amount of pulp, it was found that the wet weight of the excrement in a twenty-four hour period was nearly twice the weight of the larvae in each case. Fecal pellets are compact and disc-shaped and are easily recovered. The number of fecal pellets dropped by each third instar larva in twenty-four hours varied from 114 to 152. The average of 131 means, roughly, that each larva dropped a fecal pellet every eleven minutes. The water content of the fecal pellets averaged 84.7 per cent, which is essentially the same as the moisture content of the food before eating. The fact that the water content of food and fecal pellets is the same is of no significance in itself since the pellets are dropped in the moist food and could absorb water from it. However, the pellets are moist *when* they are dropped and before they have had time to absorb moisture from the pulp. As passalus normally lives in a moist environment the larvae do not need to conserve moisture. The work of Patterson (1937) indicates that the rectal glands, which Wigglesworth (1932) has shown to be important in some insects in re-absorbing water from fecal matter, are relatively insignificant in passalus larvae.

Prepupa and Pupa

A definite prepupal stage occurs in passalus but it is somewhat difficult to tell exactly when it begins. When the large (37 mm. - 42 mm.) third instar larvae cease feeding their color gradually changes from bluish-gray to white. While the change in color is progressing the larvae crawl about seeking a place to pupate. In the laboratory they sometimes tunnel deep into the wood pulp or soil. Again they may merely hollow out a depression on the surface by constantly turning over and over. The prepupal stage has definitely begun when these depressions are being made. The blue color has by this time completely disappeared and been replaced by a pronounced fatty appearance. Normally the adults build a pupal case about the prepupa from the old pulp in the tunnels, but in the laboratory the presence of adults is not necessary for pupation. When adults are absent pupation is accomplished without the protec-

tion of the covering case. Throughout the prepupal stage the insects are active, rolling over and over at intervals, but they make no effort to leave their depressions once they are established in them. Prepupae brought in from the woods will readily pupate in the laboratory in depressions made for them by pressing a thumb into soft earth or moist wood pulp.

The prepupal stage lasts about five days. The last larval skin is then shed and the pupa appears. It is evident that metamorphic changes begin in the prepupal stage. Late prepupae and pupae are very delicate and easily ruptured. Even small breaks in the integument lead to loss of large amounts of body fluids and subsequent death. Under natural conditions, were the prepupae and pupae not segregated from the rest of the colony by their protective cases, most would receive fatal injuries as the larvae and adults crawled over them. In logs the pupal cases are often built in the middle of the run-ways and the galleries widened so that traffic goes around them. Although pupal cases may be found anywhere in a log where there are galleries, they are found more abundantly on the under side of the log. But unlike the eggs they are seldom concentrated in any one spot.

The making of the pupal case is interesting to watch. The excellent account by Miller (1932) is the only description of this process found in the literature. The essential features of the process are as follows. When a large larva reaches the prepupal stage it selects a site and begins hollowing out a depression by constantly rolling over and over. The adults pile up the finely chewed gallery refuse around the larva and keep away all intruders, such as other third instar larvae and newly hatched adults. As material is piled up on the outside of the cocoon by the adults, the larva on the inside, by rolling and movements of its head, keeps the interior surface smooth. Miller says that the larva secretes a fluid which aids in smoothing the inner surface of the cocoon. He also says that the adults stand guard over the nearly completed cocoon, but this the writer has never observed in the natural galleries.

The pupal cases are essential for protection in the natural colonies but are not necessary for pupation. In the laboratory, if the more active large larvae and the adults are segregated from those about to begin metamorphosis, pupation will readily take place in a covered finger bowl of moist wood pulp or moist soil. It seems that the process of metamorphosis, once started, will continue uninterrupted if the larva has had proper nourishment and if the relative humidity of the environment is sufficiently high.

Nutrition and Development

The only extensive study of the food requirements of passalus larvae was made by Pearse and his collaborators (1936). These workers tried, with small success, to find the nutritional requirements by attempting to raise larvae on a large variety of diets, including different species of wood prepared in different ways, sawdust, agar preparations, and fungus cultures. Unfortunately the value of some of their experiments is somewhat lessened because they did not recognize the different larval instars and failed to note whether or not the larvae moulted; and because they did not determine the normal rate of growth on a natural diet for comparison with their data on experimental larvae. From

the measurements they give it is obvious that in some experiments first and second instar larvae were lumped together, while in others second and third instar larvae were grouped. It seems particularly unfortunate that no attempt was made to ascertain if the larvae moulted on the various diets; for, even if the larvae increased in weight, but could not moult to the next stadium, their diet was obviously not a satisfactory one. Their data in several places indicate that, although there was slow growth on a particular diet, development was delayed and ecdysis did not occur, even though the length of time involved was more than enough for the larva to have entered the next instar. In one case a larva lived 111 days; under normal conditions the whole cycle from egg to adult would have been completed in much less time. In another case the best of a group of newly hatched larvae increased in length only 5.5 mm. and in weight 164 per cent in 33 days. On their natural diet these larvae should have increased five times that much in length and about 1600 per cent in weight in 33 days, and should have reached the third instar. Few larvae on the artificial diets increased more than one hundred per cent in weight regardless of the time they were on the diet. This small increase in weight seems rather insignificant when one considers that passalus larvae on a natural diet normally increase approximately 10,000 per cent in weight before reaching the pupal stage. In other words, the artificial diets tried by Pearse and collaborators were even more unsatisfactory than their conclusions indicate. Seemingly the only really satisfactory diet they discovered was the triturated wood pulp prepared by the adults themselves. Although they do not mention it, their work also shows that the lack of a proper diet leads to a tremendous slowing of development. All of their smaller larvae and nearly all of their larger experimental larvae eventually died regardless of the diet, even though in many cases there was an increase in weight and size. If one compares the time required for such experimental larvae to increase in weight and size with the time required for normal development, it can be very readily seen that all of their larvae on experimental diets were greatly delayed in growth and metamorphosis. A few large larvae, which from their measurements must have been in the late third instar before being placed on the experimental diets, did succeed in forming pupae. Only one of these became adult, and this only after 27 days in the pupal stage. As the normal time for pupation is only 10 - 12 days, there was a developmental delay in this one stage alone of two weeks. Also, it is evident that some of the larvae were within a few days of the prepupal stage, when all feeding ceases. But even in these cases, after most of the larval life had been spent on a normal diet, the insects could not complete their transformation. Death in the pupal stage and the long delay in transformation of those that lived is hard to understand unless there was insufficient moisture. As mentioned before, larvae do not feed on food that contains much less than 85 per cent water. Also, transformation will not take place except in a humid atmosphere.

Water Relations

That water is important in the life of passalus is obvious to anyone who has observed passalus in its natural habitat or who has attempted to raise them in the laboratory. Passalus does not live in dry logs; it cannot withstand

direct sunlight; larvae will not eat dry food and succumb quickly at low humidities; and eggs absorb water during development and do not develop unless sufficient moisture is present.

Gray (1944) has followed the changes in water content of passalus from egg to adult. The moisture content of newly laid eggs averages about 68 per cent. After remaining relatively constant for about five days the water content increases steadily until, at time of hatching on the 16th day, it is about 83 per cent. Newly hatched larvae contain about 85 per cent water, but after feeding begins this increases to about 90 per cent. Throughout the three larval instars it remains practically constant, but increases slightly during the pupal stage to a high of 93 per cent. The brightly colored, newly hatched adults contain approximately 92 per cent water. The slow process of sclerotization, often requiring several months, is accompanied by a change in color and a gradual drop in water content, until, in older, black adults, a level of about 67 per cent, approximately that of newly laid eggs, is reached.

In some preliminary experiments, not yet complete enough for publication in detail, passalus in various stages of development were subjected to various humidities. The experimental animals were placed on screens in desiccators containing saturated solutions of chemicals, following the technique of Sweetman (1933). Data obtained from these brief experiments indicate one thing very definitely: at no developmental stage can passalus exist for many days at low humidities. Prepupae (within five days of forming pupae) were able to shed their last larval skin and become pupae at relative humidities as low as 65 per cent, but pupae would not transform into adults at relative humidities below 92 per cent. Third instar larvae were able to withstand lowered humidities for longer intervals than could those in first or second instars. At 75 per cent humidity first instar larvae died in two days, second instars in four days, and third instars in eleven days. Whether food was present or not made no difference, for as soon as the food dried the larvae could not make use of it. Attempts to hatch eggs in desiccators, regardless of humidity, were a failure. Even at humidities of 92 per cent and 96 per cent the eggs lost weight. These eggs were kept on wire screens in the desiccators and were not in direct contact with water. In as much as eggs can be easily raised when kept on wet filter paper or on moist wood pulp, the assumption logically follows that the eggs cannot absorb sufficient moisture from the air and must be in direct contact with water if they are to develop. While adults without food may live for fifteen days at 75 per cent humidity, they live more than twice that long at humidities of 85 per cent or 92 per cent. The water requirements of passalus need further investigation.

Parasites

Pearse and his collaborators (1936) maintain that at least sixteen species of animals live on or in *Popilius disjunctus*. These include a gregarine, two nematodes, twelve mites, and a fly. Eight new species of mites are described. They suggest the probability that ten of the twelve mites are commensals, but that the other animals are parasitic. Of the parasites two, the fly, *Zelia vertebrata*, and a nematode, *Chondronema passali*, seem especially worthy of further comment.

Zelia vertebrata. The size of a passalus colony diminishes as the season adavnces, for only a fraction of the larvae that hatch from the eggs reach maturity. There are several obstacles. Injured and weak larvae are eaten by the more healthy members of the colony. But the chief devastating agent with which passalus has to contend is the dipterous fly, *Zelia vertebrata,* which attacks the larvae.

During July and August the maggot of Zelia is very much in evidence. Passalus larvae raised from eggs or brought into the laboratory from the field in June do not become parasitized by this fly. Larvae taken in July and August, however, are very heavily infested. The fly maggot is seldom seen before July 15. Its appearance appears to be timed with the occurrence in large numbers of late third instar larvae. In late July and August, of over one thousand third instar larvae examined, 33 per cent were found to be infested with Zelia maggots. The percentage of infection ran low in some colonies, but very high indeed in others. In one group of several hundred larvae collected one day in July from several colonies 5 per cent of first instar, 30 per cent of second instar, and 60 per cent of third instar larvae had maggots in them. This is higher than usual. It is the large larvae that are most readily infected. Counts made after July 15 show that only an occasional first instar larva is attacked and 7.5 per cent of the second instar larvae. First form larvae have greatly diminished in numbers and third form larvae are increasing rapidly by the time Zelia maggots put in an appearance, so it seems quite natural to find a much greater percentage of infestation among the larger and more numerous third form larvae than among the smaller and less numerous lower forms.

The fly maggot enters the larva almost anywhere, but maintains a siphon for respiration to the surface. More than one maggot may enter a larva. In fact, it is not uncommon to find larvae with two, three, or even as many as five maggots in them. No larva parasitized by Zelia ever becomes adult. It is possible for an infected larva to moult and even to enter the pupal stage, but before transformation can be completed the maggot leaves its host to become a pupa itself. The emergence of the maggot leaves a large hole in the larva or pupa with subsequent loss of body fluids. This always results in death. Whereas 33 per cent of the third instar larvae are attacked, only 7 per cent of the pupae are infested. This means that most of the infested larvae succumb before reaching the pupal stage for, being housed in protective cases, the prepupal or pupal stages are immune from attack under natural conditions. Whereas the larvae may have multiple infection no pupa has been found with more than one maggot. Adults are free from attacks of Zelia. Whether Zelia attacks larvae other than passalus is not known. Many Scarabeid larvae live in the same logs as passalus but no infection of them has been noticed.

Chondronema passali. This nematode was first observed and described by Leidy (1852). Christie and Chitwood (1931) examined several hundred adult beetles from Maryland, Delaware, Virginia, North Carolina, Illinois, and Louisiana and found nearly all were infested. Of the few grubs examined one-fifth were infested. Although pupae were found to contain nemas, too few were studied for comparison. Christie and Chitwood concluded that the entire life cycle of Chondronema takes place in or near beetle galleries and that

adult nemas live free in the moist decayed wood or frass. They suggest that infestation is by way of mouth and that the full grown nemas leave the adult beetles only during the passalus egg-laying season. Pearse (1936) has extended our knowledge of this nematode and found that it increases in number in late summer, but that there is no month of the year when it is not present. In one instance he counted as many as 4,260 in a single beetle. The average number of nematodes in a single beetle at any season of the year he found to be 471. This seems like a heavy infestation, but one has only to open a beetle or two to be convinced. It is very startling indeed to open a fresh adult and observe the wriggling mass of nematodes in the body cavity. Only rarely is an adult found without them.

Thanks are due to Mr. James Mangrum for the data in Table 2 on the percentage of larval and pupal infestation by Chondronema. To this has been added the approximate percentage of adult infestation. It is hard to interpret the increase in percentage of infection of prepupae and pupae over third instar larvae, for in these stages no food is taken. This may mean that the small larval nemas may use other means of entering their host than by mouth. It is, however, difficult to tell when the prepupal stage actually begins and it is possible that some of the so-called prepupae may actually have been late third instar larvae. If prepupae and third instar larvae are grouped together as larvae, which in reality the prepupae are, then the percentage of infection of the larvae and of pupae is approximately the same. Too, it may be that the Chondronema larvae themselves may be much larger and more easily detected in the prepupal stage than in the earlier larval stages of passalus. No careful study has been made of the percentage of infestation of newly transformed adults, nor of the rate at which the numbers of Chondronema increase in the new adults as the latter begin feeding. Most red adults do not have as many nematodes in their body cavities as do the older black imagines. The earliest date passalus larvae were found to be infested with Chondronema was July 25. Further study should be made of the life history of Chondronema and its relation to the life history of passalus.

Mites, which are so numerous on adults, apparently do not bother the larvae and pupae. Occasionally a mite may be found crawling on a larva, but this seems to be merely accidental. Mites crawl about freely in the galleries and it is to be expected that a few get on larvae without living on them. The freedom of larvae from mites is in marked contrast to the adults. Pearse (1936) found that twelve species of mites live on passalus adults and that the average number of mites per beetle at any season of the year was 88.66.

TABLE 2.—Percentage of infestation of passalus of different stadia by the nematode, *Chondronema passali*.

Date	Stadium	Number Examined	Percent Infestation
June 1 - Aug. 5	Larva I	147	0
June 11 - Aug. 15	Larva II	208	0
June 25 - Aug. 25	Larva III	192	5
July 25 - Aug. 25	Prepupa	62	29
July 29 - Sept. 15	Pupa	130	35
	Old Adults		95

Animal Associates

Many animals take advantage of the tunnels made by passalus and make temporary or permanent homes in them. In addition to the twelve species of mites that live on the adult passalus, the two species of nematode that live within them, and the fly that parasitizes the larvae, there are many other animals that at one season or another live as transients in the burrows. Among animals commonly found are nematode and annelid worms; insects belonging to the orders Collembola, Thysanura, Orthoptera, Coleoptera, Hymenoptera, and Diptera; salamanders, lizards, and snakes. Annelid egg-cocoons are common in the moist wood pulp in June. The slimy salamander (*Plethodon glutinosus*) often, and the red eft (*Triturus v. viridescens*) occasionally, are found hiding in the burrows. The blue-tailed skink (*Eumeces fasciatus*) frequently, and sometimes the pine lizard (*Sceloporus undulatus*) also, makes use of those tunnels that are close under the bark for egg laying. Eggs of the ring-neck snake (*Diadophis punctatus*) and of the ground snake (*Potamophis striatulus*) have been taken from passalus burrows deep within oak logs. Adult beetles have been observed to bite into termite runways and even to eat termites that got in the pathway of their moving jaws. Termites, however, prefer their own runways and are only accidental and temporary inhabitants of passalus galleries. A detailed study of passalus tunnels should reveal a large number of animals living there.

Social Life and Communication

Both adult and larva possess organs of stridulation. Those of the adult have been accurately described by Babb (1901), who disproved the statements of Riley (1872), LeConte (1878), and Ohaus (1900), that the elytra were directly concerned with sound production. A pair of ovate areas, not unlike a rasp, on the fifth abdominal tergite are rubbed against special sclerotized folds of the under wings when the abdomen is raised. The sound thus produced is a rather sharp squeak. The only part played by the heavy elytra in sound production is to hold the under wings in position. The organs of stridulation are the same for both sexes.

To those who have handled passalus the statement of Sharp (1901) is of interest. After illustrating the stridulating organ of a larval passalid he says, "The perfect insect has no sound-producing organs, and it is very remarkable therefore to find the larvae provided with highly-developed stridulatory structures."

Larval stridulatory organs seem to be quite similar in the different members of the family Passalidae. They consist of a modified third leg, shaped like a bear paw, that is vibrated rapidly over a striated area on the middle coxa. The sound produced is feeble, but can be distinctly heard if the larva is held close to the ear. By comparison the adult makes loud sounds when disturbed and louder still when fighting.

Ohaus (1900) from his study of South American passalids, was convinced that stridulation served as a means of communication between members of the

colony and described some remarkable cases of larvae following the calls of the parents. On the other hand Gravely (1915) from his observations on oriental species, found no evidence that stridulation was used as a means of communication. He thinks that the adults stridulate when disturbed, presumably in order to drive off an enemy. As for *P. disjunctus* Wheeler and Bailey (1920) and Pearse (1936) support the view of Ohaus, while Babb (1901) agrees with Gravely—that stridulation is an evidence of the insect's displeasure at being disturbed. Many years of observation have convinced the writer that communal life in *P. disjunctus* has not developed to the high degree of perfection described by Ohaus for some South American species. Certainly the larvae do not follow closely after the adults as they move about the tunnels, nor do the adults call their larvae to them in the manner of a hen clucking for her chickens, as Ohaus has depicted for certain Brazilian passalids. The horned passalus does not emit sounds constantly, even when it has a brood to look after, and is seldom heard except when disturbed. On being disturbed, however, it does emit loud sounds that may serve as a signal of danger to others in the colony. Also, its stridulation may be a warning to intruders from other colonies who attempt to encroach on their neighbors. Sound produced when angry, as in vigorous fighting, is much louder and more emphatic than when the beetles are merely disturbed. This difference is easily distinguishable. Larvae, also, stridulate violently when disturbed. Larval stridulation, which is more or less continuous, may serve to keep adults informed of the location of the young, for members of a colony are often separated by many feet in the more extensive galleries. Undoubtedly stridulation does aid in keeping the colony together, but the writer is not convinced that it is used in obtaining mutual cooperation or that inter-communication in *Popilius disjunctus* colonies has developed to such a degree that members of the colony are able to express specific needs and desires to one another, as indicated by Wheeler and Bailey (1920) for certain species of ants.

Economic Importance

While passalus cannot be listed among the insects of great economic importance, it does play a part in hastening the decomposition of rotting logs in the forest and reducing them to humus. As passalus lives only in rotting logs it does not attack well-seasoned timber. It will, however, tunnel into logs used for the support of bridges in moist places and hasten the condemnation of the bridges. Passalus will not attack living or freshly cut timber. As shown by Savely (1939) oak logs must be at least two years old before passalus enters.

Summary

Passalus spends practically its whole life in rotting hardwood logs. The developmental history from egg to adult is completed in 2½ to 3 months during the summer season. There is but one generation per year. Each female lays approximately thirty large red eggs over a period of two or more weeks. The eggs change color and increase in size, weight, and water content during the 16 days required for their development. Approximately 12, 10, and 25

days, respectively, are spent in the three larval instars. A prepupal stage of 5 days and a pupal stage of 10 - 12 days are spent within the pupal case. The pupal case is made by the adults assisted from within by the larva. Food requirements, water relations, parasites and other animal associates, social life, and economic importance are discussed. The chief enemy of passalus is the parasitic fly, *Zelia vertebrata,* which causes the death of a third of the late third instar larvae.

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The Ants of Northeastern Minnesota[1]

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Whereas over 90 species of ants (including subspecies and varieties) are known from that part of the Upper Austral Zone in the vicinity of Chicago, Illinois (Gregg 1944), as yet only 40 species are represented in our collection of the Lake Superior district and constitute the basis of this paper. The localities where ants were obtained lie entirely within the Canadian Zone, and the specimens illustrate well the typical ant fauna of a northern climate. Some forms characteristic of the more southern area are present in Duluth but seem not to be as conspicuous, and many of their associates in Illinois are completely absent from Duluth, as would be expected. They have been replaced by boreal types not found at all or only rarely south of the coniferous forests. It appears that most of the timber in this portion of Minnesota is of second growth, and while new evergreen forests are developing, many square miles are occupied by aspen communities. The precise nature of the myrmecological changes that have accompanied the floristic ones it is at present impossible to state, but the monotonous aspect of the ant fauna in certain examples of the typical vegetation (spruce-tamarack bogs and stands of upland conifers), as compared with the greater number of varieties in deciduous woodland and the many forest margins, leads one to suspect that the fauna is more mixed than prior to the disturbance of the forest cover.

In the following list there are probable omissions which further collecting would fill, but it is felt that such an enumeration is justified in view of the scant literature concerning the ant populations in this section of the country. Wheeler (1908) published an account of ten species taken on Isle Royale, Michigan, and almost all are of a distinctly northern distribution. Burrill and Smith (1918, 1919) provided a guide to the ants of Wisconsin and recognized 46 species from that state. There seem to have been no papers other than these devoted to the ants of the upper lake region. The extensive records in Wheeler's (1913) key to the *Formicae* contain no references to Minnesota localities though citations from all the surrounding states and Canadian provinces must be admitted.

For Minnesota vegetation see Rosendahl and Butters 1928.

1 The materials for this report were gathered with the help of my wife over a period of several years, and except for the specimens obtained at the southern tip of Saganaga Lake, Minnesota, represent mostly the findings in local spots in and near Duluth. We are greatly indebted to Dr. Olga Lakela for her enthusiastic assistance in collecting and for her generosity in making known to us the many natural areas in this part of the state, which otherwise we would never have been able to visit. A few specimens have been contributed by Reino Freeman, Axel Wiljamaa, Irma Roine, Warren Annis, Joseph Zygmanski, Helen Poynter and Ingrid Lahtinen, and acknowledgment of these is made in connection also with the species named. Dr. C. E. Mickel kindly permitted me to examine the ant collection at the University of Minnesota, and arranged for me an exchange of certain specimens.

PONERINAE

1. *Ponera coarctata pennsylvanica* Buckley[2]

Minnesota: Saganaga Lake.
Habitat: coniferous forest; log stage 53; under rock.
Collections: 2.

The species seems to be present only sporadically in this northern region, and thorough examination of various micro-habitats did not reveal more than a few specimens.

MYRMICINAE

2. *Aphaenogaster tennesseensis* (Mayr)

Minnesota: Hovland (Poynter).
Collections: 1.

Despite careful search for members of the genus, we can record only a single individual of this species, and no habitat data were provided by its collector. Inasmuch as *tennesseensis* is known to be a temporary parasite on species of *A. fulva*, it is possible to predict that the latter should eventually be found in the area.

3. *Harpagoxenus canadensis* M. R. Smith

Minnesota: Duluth (Freeman, Wiljamaa, Zygmanski, Gregg).
Habitat: basswood-maple forest, tamarack-spruce bog; log stages 2 and 3.
Collections: 5.

Two of the colonies had a considerable quantity of brood, and they were associated with *Leptothorax acervorum canadensis* which acts as a slave species.

4. *Leptothorax texanus* Wheeler

Minnesota: Duluth (Wiljamaa).
Habitat: basswood-maple forest.
Collections: 1.

The species appears to be far north of its usual range, and as yet only one specimen has been taken.

5. *Leptothorax* (*Mychothorax*) *acervorum canadensis* Provancher

Minnesota: Duluth, Saganaga Lake.
Habitat: basswood-maple forest, aspen forest, tamarack bog, spruce-fir forest, Lake Superior shore rocks; log stage 2.
Collections: 10.

Most of the records are represented by isolated individuals, but one colony had well developed brood and two others were with the nests of *Harpagoxenus*.

6. *Myrmica schencki emeryana* Forel

Minnesota: Duluth (Freeman, Roine, Gregg), Rice Lake, Holyoke, Knife River, Saganaga Lake.
Wisconsin: Superior, Foxboro.
Habitat: coniferous forest, tamarack bog, basswood-maple forest, oak-ash forest, aspen forest, forest margin, pioneer dunes; log stages 3, 4 and 6; under rocks, sticks and logs, also moss covering rocks.
Collections: 33.

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2 The third word in trinomials is understood to indicate a subspecies.

3 See Gregg (1944) for description of log stages.

This is an exceedingly common ant and is apparently adaptable to a wide variety of conditions. Almost all the records represent thriving colonies and many of them had clusters of brood. Seven nests had examples of the winged sexes.

7. *Myrmica sabuleti americana* Weber

Minnesota: Duluth (Freeman, Roine, Gregg), Saganaga Lake.
Habitat: coniferous forest, pioneer dunes.
Collections: 9.

In contrast to the preceding species, this ant seems to be much rarer and a few foraging individuals constitute the bulk of our material.

8. *Myrmica brevinodis* Emery

Minnesota: Duluth, Knife River, Saganaga Lake.
Wisconsin: Superior.
Habitat: coniferous forest, tamarack-spruce bog, cedar bog, basswood-maple forest, aspen forest, pioneer dunes, Lake Superior shore rocks; log stages 3, 4 and 5; under rock and wood.
Collections: 10.

Together with *M. s. emeryana* this species characterizes the evergreen woodlands and is well represented in many of the older communities in the region.

9. *Myrmica brevinodis brevispinosa* Wheeler

Minnesota: Duluth, Holyoke.
Habitat: coniferous forest, oak-ash forest.
Collections: 5.

Closely related to the foregoing species but much less abundant. Three specimens were found foraging on vegetation in proximity to two individuals of the ant mimic, *Sericophanes heidemanni* Poppius? (Heteroptera).

10. *Myrmica brevinodis canadensis* Wheeler

Minnesota: Duluth, Holyoke, Knife River, Carlton Co., Saganaga Lake.
Habitat: coniferous forest, coniferous-maple forest, maple-basswood forest, Lake Superior shore rocks; log stages 3, 4 and 5.
Collections: 7.

11. *Stenamma brevicorne impressum* Emery

Minnesota: Saganaga Lake.
Wisconsin: Foxboro.
Habitat: birch forest, forest margin: log stages 4 and 5.
Collections: 2.

This form is always uncommon, or at least its hypogaeic habits lend it that aspect, but the two colonies obtained were very populous and one had a large mass of brood.

DOLICHODERINAE

12. *Dolichoderus* (*Hypoclinea*) *taschenbergi aterrimus* Wheeler

Minnesota: Duluth.
Habitat: Lake Superior shore rocks.
Collections: 1.

This ant was taken as it ran about a few feet above the waves on the lake shore. Only two dealated females were secured, and the occurrence of the species in this latitude is problematical since its relatives are notably southern types and no established colony was discovered.

13. *Tapinoma sessile* (Say)

Minnesota: Duluth (Zygmanski, Gregg), Holyoke, Knife River, Saganaga Lake.
Habitat: coniferous forest, birch-conifer ravine, aspen forest, oak-maple forest, basswood-maple forest, forest margin, Lake Superior shore rocks; log stage 2; under rocks.
Collections: 11.
This is the only important example of the subfamily in boreal localities.

FORMICINAE

14. *Lasius niger neoniger* Emery

Minnesota: Duluth, Holyoke.
Habitat: coniferous forest, birch-conifer ravine, foredunes, oak-ash forest.
Collections: 4.

It is less widely distributed than the following species, and the best colonies were in relatively warm situations on sand.

15. *Lasius niger americanus* Emery

Minnesota: Duluth, Holyoke, Carlton Co., Saganaga Lake.
Wisconsin: Foxboro.
Habitat: coniferous forest, maple-conifer forest, oak-maple forest, forest margin, pasture; log stages 2, 3 and 4; under rocks and wood.
Collections: 16.

As would be expected, this eurokous ant is a conspicuous member of the biota. It occupies a broad range over the North American continent.

16. *Lasius niger sitkaënsis* Pergande

Minnesota: Duluth. Holyoke.
Habitat: coniferous forest, birch-conifer ravine, oak-ash forest; under wood.
Collections: 6.

One of the most typical of northern insects, and to my knowledge does not occur south of the Transition Zone. It was originally described from Alaska.

17. *Lasius* (*Chthonolasius*) *umbratus aphidicola* (Walsh)

Minnesota: Duluth.
Habitat: pioneer dunes.
Collections: 1.

The data for this species are not particularly reliable as one wingless female was captured wandering over the sand on Minnesota Point, and no nests of the ant have been located thus far.

18. *Formica* (*Proformica*) *neogagates vetula* Wheeler

Minnesota: Duluth, Holyoke.
Wisconsin: Foxboro.
Habitat: birch-conifer ravine, basswood-maple forest, oak-ash forest, forest margin, pioneer dunes.
Collections: 6.

It is present in tolerable numbers, but the typical form of the species which occurs commonly in the same habitats with this subspecies in Illinois seems to be entirely absent from the Duluth area.

19. *Formica* (*Proformica*) *limata* Wheeler

Minnesota: Carlton.
Habitat: log stage 3.
Collections: 1.
Originally described from fairly high altitudes in Colorado, hence its occurrence in the northern part of the eastern states is not surprising.

20. *Formica cinerea neocinerea* Wheeler

Minnesota: Duluth.
Collections: 1.

Although this ant is a predominant one in the prairies of the central United States it was secured on but one occasion in eastern Minnesota, and is probably at the edge of its normal distribution. It is possible that with the destruction of continuous forest and the development of grassland conditions, the species has extended into the Lake Superior district.

21. *Formica fusca* Linnaeus

Minnesota: Duluth (Annis, Gregg).
Habitat: basswood-maple forest, spruce bog, forest margin.
Collections: 4.

This species is remarkable for its circumpolar, boreal distribution. However, it was found to be less abundant in Duluth area than I had suspected, and fewer records of it were obtained than of some of its subspecies.

22. *Formica fusca subaenescens* Emery

Minnesota: Duluth (Roine, Wiljamaa, Gregg), Carlton, Holyoke, Knife Island, Saganaga Lake.
Habitat: coniferous forest, spruce-fir forest, basswood-maple forest, aspen forest, oak-maple forest; log stages 3 and 4.
Collections: 14.

An ant of the northern climate, and in mountainous regions it reaches high elevations. It is more frequently encountered than in the Illinois collections, and in the latter state is correlated with cool and shady stations.

23. *Formica fusca subsericea* Say

Minnesota: Duluth, Rice Lake, Holyoke, Hovland (Poynter), Saganaga Lake.
Wisconsin: Foxboro.
Habitat: coniferous forest, spruce-fir forest, oak-ash forest, tamarack bog, aspen forest, forest margin; log stage 3; under rocks and logs.
Collections: 19.

This insect is tolerant of great variations in its environment, and occurs over almost all of eastern United States with an extension into the southwest. It is one of the most suitable species for use as slaves by ants of the *sanguinea* group.

24. *Formica fusca algida* Wheeler

Minnesota: Duluth, Carlton, Carlton Co., Saganaga Lake.
Wisconsin: Foxboro.
Habitat: tamarack bog, coniferous forest, spruce-fir forest, maple-conifer forest; log stages 2, 3, 4, and 5; under rock.
Collections: 18.
Known from peat bogs in boreal North America from the Atlantic Coast to western Ontario and eastern Minnesota. The author's experience shows, however, that it is not limited to bogs, because fully as many colonies were collected in cool northern woods of upland character as from tamarack swamps. In our collecting it was one of the most conspicuous forms and shared its dominance among the *fusca* group chiefly with *subsericea*.

25. *Formica fusca gelida* Wheeler

Minnesota: Saganaga Lake.
Wisconsin: Foxboro.
Habitat: coniferous forest, forest margin; log stages 2, 4.

Collections: 3.

As Wheeler has shown, this ant is diagnostic for high latitudes and for high altitudes. Though it is typical of the mountains of western United States and Canada, and is there restricted to high altitudes, three of its colonies were discovered in Minnesota. This seems very unusual, but it is not an impossibility, and the specimens would indicate an eastward extension of its range perhaps through the boreal portions of Canada to the point where it overlaps with its eastern relative, *F. f. algida*.

26. *Formica sanguinea aserva* Forel

Minnesota: Duluth (Wiljamaa, Gregg), Carlton, Holyoke, Knife River, Saganaga Lake.

Wisconsin: Foxboro.

Habitat: coniferous forest, maple-basswood forest, birch forest, aspen forest, forest margin, pasture, pioneer dunes; log stages 3, 4 and 5; under rock.

Collections: 24.

This is the usual slave-maker among the northern ants, but its colonies often are without auxiliaries. The young queen is known, however, to establish her colony by invading the nest of a species of *fusca*. Owing to the failure of making dulotic raids, her worker offspring gradually allow the colony to become a pure *aserva* community.

27. *Formica sanguinea subnuda* Emery

Minnesota: Duluth, Saganaga Lake.

Wisconsin: Foxboro.

Habitat: coniferous forest, birch-conifer ravine, aspen forest, forest margin; log stage 4; under log.

Collections: 6.

This is also an evergreen forest inhabitant and at times is found in alpine situations, but it is not prominent in our fauna to judge from the few records we have in the area.

28. *Formica pergandei* Emery

Minnesota: Saganaga Lake.

Habitat: coniferous forest; log stage 4.

Collections: 1.

According to Wheeler this member of the *sanguinea* group is very rare, and indeed we have seen it only on one occasion. There seems to be some question as to whether it normally has slaves, but the nest we collected was mixed and the auxiliaries belong to *F. fusca subsericea*.

29. *Formica emeryi* Wheeler

Minnesota: Saganaga Lake.

Habitat: coniferous forest.

Collections: 1.

Another member of the *sanguinea* group and very similar to *pergandei*. A single worker is in our possession.

30. *Formica ulkei* Emery

Minnesota: Duluth, Carlton, Carlton Co.

Wisconsin: Foxboro.

Habitat: basswood-maple forest, forest margin, meadow.

Collections: 9.

The species seems to be an indicator of forest margin or artificially induced marginal conditions such as roadsides and trails. Whereas in Illinois its occurrence is very local and unpredictable, in upper Minnesota is common in suitable situations.

31. *Formica rufa gymnomma* Wheeler

Minnesota: Duluth, Beaver Bay, Saganaga Lake.
Habitat: coniferous forest, spruce-pine forest, forest margin, pioneer dunes.
Collections: 8.

This important eastern member of the *rufa* group is well exemplified in the survey made, but most records of its distribution in America would probably show it to be more characteristic of the Transitional and Upper Austral life belts.

32. *Formica oreas comptula* Wheeler

Minnesota: Saganaga Lake.
Habitat: coniferous forest, spruce-fir forest.
Collections: 5.

This species and the typical form are distinctly western ants, but with the present records it seems to mix with the eastern fauna to a certain extent.

33. *Formica whymperi adamsi* Wheeler

Minnesota: Duluth.
Habitat: spruce bog.
Collections: 2.

Another form sparingly represented in the vicinity of Duluth but supposedly at home in northern climates and high altitudes.

34. *Formica dakotensis* Emery

Minnesota: Duluth.
Habitat: spruce bog.
Collections: 1.

This ant and its subspecies which follows are quite uncommon, and it was only by chance we obtained a few individuals.

35. *Formica dakotensis montigena* Wheeler

Minnesota: Duluth.
Habitat: spruce bog, forest margin.
Collections: 3.

36. *Camponotus herculeanus whymperi* Forel

Minnesota: Duluth (Lahtinen, Gregg), Angora (Roine), Rice Lake, Holyoke, Knife Island, Saganaga Lake.
Wisconsin: Superior.
Habitat: coniferous forest, tamarack bog, birch-conifer ravine, aspen forest, oak-maple forest; log stages 3 and 4; under rocks.
Collections: 25.

This is the exceedingly common carpenter ant of the north woods replacing *C. herculeanus pennsylvanicus* of the middle and southern states. It ranges completely across the continent in the boreal forests and in places reaches into the Transition Zone.[4]

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4 Carpenter ants were found abundantly attacking sound timber in the white cedar stands of Minnesota (S. A. Graham, 1918), and this was regarded as unusual inasmuch as it had not been reported for *Camponotus herculeanus pennsylvanicus* nor for the subspecies *ferrugineus*. These forms do not occur in the coniferous forest, and the infestation may undoubtedly be traced to the northern subspecies *whymperi*, and possibly to the subspecies *noveboracensis* also.

37. *Camponotus herculeanus noveboracensis* (Fitch)

Minnesota: Duluth, Holyoke, Knife River, Knife Island, Saganaga Lake.
Wisconsin: Foxboro.
Habitat: coniferous forest, birch-conifer ravine, maple-basswood forest, red oak forest, oak-ash forest, aspen forest, pioneer dunes, forest margin, meadow, Lake Superior shore rocks; log stages 2, 4 and 5.
Collections: 15.

Again a northern ant but not as stenothermal as *whymperi*. It is very common in the subboreal and austral localities, and has a wide dissemination from east to west.

38. *Camponotus* (*Myrmentoma*) *caryae nearcticus* Emery

Minnesota: Duluth.
Habitat: floodplain thicket; log stage 4.
Collections: 1.

As far as our experience shows, this ant is the only sample of the *caryae* group in the area, and it was taken on just one occasion. Its main distribution is to the south.

39. *Polyergus rufescens bicolor* Wasmann

Minnesota: Saganaga Lake.
Habitat: spruce-fir forest.
Collections: 1.

The specimens taken were on an out-bound raid as they crossed a road and disappeared into thick grass. Despite repeated efforts to locate the nest we were unsuccessful, and consequently were unable to secure additional material.

40. *Polyergus rufesecns fusciventris* Wheeler

Minnesota: Duluth.
Habitat: tamarack-spruce bog.
Collections: 1.
Isolated specimens collected accidentally with other ants.

In summarizing some of the data in the foregoing list, it may be useful to specify the ants which are distinctly boreal (leaving out of consideration those that are borderline cases), and to compare that assemblage with the austral fauna particularly in regard to those species which are absent from the Duluth area.

Northern Species

Leptothorax acervorum canadensis
Harpagoxenus canadensis
Myrmica brevinodis
Lasius niger sitkaensis
Formica fusca
Formica fusca subaenescens
Formica fusca algida
Formica sanguinea aserva
Formica ulkei
Formica whymperi adamsi
Formica dakotensis montigena
Camponotus herculeanus whymperi

One species of *Dolichoderus* and one of *Aphaenogaster* have been found in the north as the survey indicates, and additional ones of the latter genus are expected. With these two exceptions, the following fourteen genera of Eastern United States are entirely absent from northern Minnesota, (though present in Illinois), and represent a total of twenty-six species having a more southern distribution.

Stigmatomma
Aphaenogaster
Crematogaster
Solenopsis
Monomorium
Myrmecina
Strumigenys
Pheidole
Iridomyrmex
Dorymyrmex
Dolichoderus
Brachymyrmex
Paratrechina
Prenolepis

Even the common holarctic genera contain numerous species which do not establish themselves beyond the limits of the deciduous forest and grassland belt, and the most important of these may be cited.

Lasius brevicornis
Lasius flavus nearcticus
Lasius umbratus aphidicola ?
Lasius claviger
Lasius interjectus
Lasius latipes
Formica exsectoides
Formica rufa melanotica
Formica sanguinea rubicunda
Formica sanguinea subintegra
Formica pallidefulva spp.
Formica neogagates
Camponotus castaneus
Camponotus castaneus americanus
Camponotus herculeanus pennsylvanicus
Camponotus herculeanus ferrugineus
Camponotus caryae tanquaryi
Camponotus caryae discolor
Camponotus caryae subbarbatus

Several species, resting on the capture of single individuals, have been included as members of our fauna, but these will have to be confirmed by the discovery of flourishing colonies. The *Dolichoderus* . . . *aterrimus* and *Lasius* . . . *aphidicola* records conceivably could be accounted for as stray ants blown by a strong wind from distant nuptial flights. In both instances only dealated females were caught as they wandered apparently in search of nesting sites. At no time have colonies of these species been found.

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Helminth Parasites of Birds and Mammals in Western Massachusetts

John S. Rankin, Jr.

Little is known of the helminths parasitic in wild birds and mammals of New England. Although a few isolated papers on single species occur in the literature, no reports of extended surveys for such parasites have been encountered. The importance of understanding the distribution of wild animal parasites has been indicated by many writers (Cameron, 1935; Van Cleave, 1937; etc.). Wild animals may act as reservoir hosts for domestic animal parasites. Some helminths may affect the distribution of animals seasonally and geographically. The health and vitality of wild animals may be seriously affected. Any data concerning the occurrence of such parasites are of importance in outlining conservation and control measures. It is hoped that the present survey may be of help to future investigators in indicating what helminth parasites are present in western Massachusetts, as well as to extend the known distribution of these worms.

While associated with the Biology Department of Amherst College, Amherst, Massachusetts, opportunity was had to study most of the common vertebrates in that region. A report on the helminths parasitic in Amphibia and Reptilia is appearing elsewhere (Rankin, 1945). The present paper is concerned with a report of the helminth fauna observed in birds and mammals. The writer was most fortunate in obtaining the cooperation of various hunters and trappers, who, after skinning the animals, arranged for collection of carcasses. Mr. John Harlow, curator of the Geology Department at Amherst College, was extremely helpful in contacting trappers and in supplying personally animals for study. Dr. E. E. Wehr and Dr. E. W. Price, of the U. S. Bur. Animal Industry, identified most of the nematodes collected. Dr. H. J. Van Cleave, of the University of Illinois, identified the acanthocephalan, *Moniliformis clarki*. Sincere appreciation is expressed for their valuable help.

49 birds, representing nine different species, and 122 mammals, representing 14 different species, were examined. 40 species of helminths were obtained: 17 nematodes, 13 cestodes, eight trematodes, and two acanthocephalans.

No reference is made to questions of technique as an account of the methods used in handling parasitic helminths has been published previously (Rankin, 1945).

The classification of the mammals adopted here is that used in Pratt's "Manual of the Vertebrates of the United States" (1935); of the birds, the A. O. U. Check List of North American Birds; of the major classification of the helminths, that of Pearse's List of Zoological Names (1936).

An asterisk before the name of the helminths indicates a new distribution record.

Summary of Hosts Examined

The following table includes a summary of hosts examined and parasites found.

BIRDS

Host	No. Examined	Parasite	No. Hosts infected
Capella delicata (Ord). (Wilson's Snipe)	1	*Anomotaenia variabilis*	1
Bonasa u. umbellus (L.) (Eastern Ruffed Grouse)	18	*Ascaridia bonasae*	8
Philohela minor (Gmelin). (American Woodcock)	11	*Nematostrigea* sp.	3
		Echinostome sp.	1
		Anomotaenia variabilis	4
		Acanthocephalan	1
Phasianus colchicus torquatus Gmelin. (Ring-necked Pheasant)	12	*Heterakis gallinae*	9
Cyanocitta c. cristata (L.) (Northern Blue Jay)	2	Negative	0
Corvus b. brachyrhynchos Brehm. (Eastern Crow)	2	*Anomotaenia constricta*	1
Dendroica c. caerulescens (Gmelin). (Black-throated Blue Warbler)	1	Negative	0
Strix v. varia Barton. (Northern Barred Owl)	1	*Anomotaenia constricta*	1
Accipiter v. velox (Wilson) (Sharp-shinned Hawk)	1	*Ascaridia galli*	1

MAMMALS

Sylvilagus floridanus transitionalis (Bangs). (Common Rabbit)	2	*Cittotaenia variabilis*	1
		Cysticercus (Taenia) pisiformis	2
		Obeliscoides cuniculi	1
		Passalurus ambiguus	1
Tamias striatus (L.). (Eastern Chipmunk)	2	*Capillaria* sp.	1
Sciurus carolinensis leucotis (Gapper) (Northern Gray Squirrel)	20	*Cittotaenia pectinata americana*	1
Sciurus hudsonicus gymnicus Bangs. (Common Red Squirrel)	2	Negative	0
Rattus norvegicus (Erxleben). (Common Rat)	10	*Capillaria plica*	2
		Trichinella spiralis larvae	2

Ondatra zibethica (L.). (Muskrat)	6	*Echinostoma revolutum*	4
		Plagiorchis proximus	2
		Cysticercus (Taenia) pisiformis	3
		Hymenolepis evaginata	1
Mephitis nigra (Peale and Beauvois). (Common Skunk)	19	*Alaria intermedia*	6
		Oochoristica mephitis	14
		Ascaris columnaris	15
		Crenosoma zederi	6
		Physaloptera maxillaris	19
		Moniliformis clarki	1
Procyon l. lotor (L.). (Raccoon)	2	*Mesocestoides variabilis*	1
Erethizon dorsatum (L.). (Porcupine)	1	*Schizotaenia americana*	1
		Wellcomia evoluta	1
Mustela n. noveboracensis (Em.). (Common Weasel)	1	Negative	0
Urocyon c. cinereo-argenteus (Schreber). (Gray Fox)	2	*Alaria arisaemoides*	1
		Alaria intermedia	1
		Dipylidium caninum	1
		Oochoristica mephitis	1
		Taenia pisiformis	2
		Toxocara canis	1
		Uncinaria stenocephala	1
Vulpes fulva (Desmarest). (Eastern Red Fox)	4	*Alaria arisaemoides*	2
		Capillaria aerophila	2
		Capillaria plica	2
		Crenosoma vulpis	1
		Physaloptera sp. larvae	1
		Toxocara canis	1
		Uncinaria stenocephala	4
Myotis l. lucifugus (LeConte). (Little Brown Bat)	1	*Acanthatrium nycteridis*	1
		Limatulum gastroides	1
		Plerocercoid larvae	1
Odocoileus v. virginianus (Bod.) (Virginia Deer)	1	*Moniezia expansa*	1

Helminths Encountered

Phylum: PLATYHELMINTHES Gegenbaur, 1859
Class: TREMATODA Rudolphi, 1808
Sub-Class: DIGENEA Carus, 1863
Order: STRIGEATOIDEA LaRue, 1926
Sub-Order: STRIGEATA LaRue, 1926
Family: STRIGEIDAE Railliet, 1919
Sub-Family: ALARIINAE Hall and Wigdor, 1918

1. ALARIA ARISAEMOIDES Augustine and Uribe, 1927

Hosts: *Urocyon c. cinereoargenteus, Vulpes fulva.*
Position: Jejunum.

As far as can be determined, this is only the second time that this species has been recorded since the original description by Augustine and Uribe

(1927). As many as 22 specimens were taken from a single red fox (*V. fulva*). Most of the worms found were much larger than those described by the original authors, some reaching a length of 11 mm. The lumen of the gut, in one instance, was so clogged by the worms present that little space seemed available for passage of food. No other helminths were found in the same region of the gut.

2. *ALARIA INTERMEDIA Olivier and Odlaug, 1938

Hosts: *Urocyon c. cinereoargenteus, Mephitis nigra.*
Position: Duodenum.

Odlaug (1940) described the morphology and life cycle of this trematode, based entirely on experimental data. No natural infection with the adult was indicated. The present record is apparently the first account of a natural infection. The worms found agree in all respects with Odlaug's description. One gray fox (*U. c. cinereoargenteus*) harbored 75 specimens. Six out of 19 skunks (*M. nigra*) were infected, one with 198 worms. In the latter instance, the upper end of the duodenum, immediately below the stomach, was thickly dotted with the worms. Small hemorrhagic areas were present.

Sub-Family: STRIGEINAE Railliet, 1919

3. *NEMATOSTRIGEIA Sandground, 1934

Host: *Philohela minor.*
Position: Duodenum.

A single specimen of a strigeid was recovered from an American Woodcock. Partial disintegration prevented specific identification. Careful study, however, showed that it belonged to the genus *Nematostrigeia*, very near if not identical to *N. serpens* (Nitzsch, 1819) Sandground, 1934. Sandground recorded it from various birds in Southern Rhodesia and Europe. As far as can be determined, this is the first instance of its presence in this country.

Order: PROSOSTOMATA Odhner, 1905
Sub-Order: DISTOMATA Zeder, 1800
Family: ECHINOSTOMIDAE Looss, 1902
Sub-Family: ECHINOSTOMINAE Looss, 1899

4. ECHINOSTOMA REVOLUTUM (Froelich, 1802)

Host: *Ondatra zibethica.*
Position: Duodenum.

A trematode of world-wide distribution, *E. revolutum* occurs commonly in muskrats in the Amherst area. The life cycle has been described by Johnson (1920) and Beaver (1937). Notes on the life cycle and ecology of this fluke were published by Rankin (1939).

5. "Echinostome."

Host: *Philohela minor.*
Position: Duodenum.

The state of disintegration was too great to allow for positive identification.

Family: PLAGIORCHIIDAE Luhe, 1901, emend. McMullen, 1937
Sub-Family: PLAGIORCHIINAE Pratt, 1902, emend Olsen, 1937

6. *PLAGIORCHIS PROXIMUS Barker, 1915

Host: *Ondatra zibethica.*
Position: Duodenum.

As many as 250 specimens of this trematode were found in a single muskrat. Since its first description by Barker (1915), *P. proximus* has been found commonly in muskrats, although Penn (1942) did not mention it in his survey of Louisiana muskrats. The life cycle was completed by McMullen (1937).

Family: LECITHODENDRIIDAE Odhner, 1910
Sub-Family: LECITHODENDRIINAE Looss, 1896

7. *ACANTHATRIUM NYCTERIDIS Faust, 1919

Host: *Myotis l. lucifugus.*
Position: Duodenum.

Two specimens of *A. nycteridis* were found in a single bat. Since the erection of the genus by Faust (1919) several species have been described in this country. A description of new species, with a key to known species of the genus, was published by Macy (1940). The writer does not agree with Bhalerao (1936) who suggested that the genus *Acanthatrium* be considered a synonym of the genus *Prosthodendrium* Dollfus, 1931.

8. *LIMATULUM GASTROIDES Macy, 1935

Host: *Myotis l. lucifugus.*
Position: Duodenum.

Two specimens of *L. gastroides* were found in a single bat. Macy (1935) described this fluke from bats in Wisconsin. The present record extends the known distribution of *L. gastroides* to New England.

Class: CESTOIDEA Rudolphi, 1808
Sub-Class: CESTODA van Beneden, 1849
Superfamily: TAENIOIDEA Zwicke, 1841
Family: DILEPIDIDAE Railliet and Henry, 1909
Sub-Family: DILEPIDINAE Railliet and Henry, 1909

1. *ANOMOTAENIA VARIABILIS (Rudolphi, 1802) Cohn, 1900

Hosts: *Capella delicata, Philohela minor.*
Position: Intestine.

A single snipe contained 275 specimens. 36% of the woodcocks were infected. Some lesions and light hemorrhages were evident.

2. *ANOMOTAENIA CONSTRICTA (Molin, 1858)

Hosts: *Strix v. varia, Corvus b. brachyrhynchos.*
Position: Intestine.

A few specimens were found in each host. Wardle (1933) reported this tapeworm as common in crows in Manitoba.

Sub-Family: DIPYLIDINAE Stiles, 1896

3. DIPYLIDIUM CANINUM (Linnaeus, 1758) Railliet, 1892

Host: *Urocyon c. cinereoargenteus.*
Position: Duodenum.

553 specimens of this common dog tapeworm were found in a gray fox. The lumen of the gut was clogged almost shut. *D. caninum* was found commonly in local dogs and cats.

Family: ANOPLOCEPHALIDAE Cholodkowsky, 1902
Sub-Family: ANOPLOCEPHALINAE Blanchard, 1891

4. *CITTOTAENIA VARIABILIS (Stiles, 1895) Stiles and Hassall, 1896

Host: *Sylvilagus f. transitionalis.*
Position: Duodenum.

A single specimen of *C. variabilis* was found in a rabbit. Arnold (1938) recorded it from species of *Sylvilagus* in Northeastern United States.

5. *CITTOTAENIA PECTINATA AMERICANA Douthitt, 1915

Host: *Sciurus c. leucotis.*
Position: Intestine.

A single specimen of this tapeworm was found in one out of 20 gray squirrels examined. Harkema (1936) recorded it from *Sylvilagus* sp. in North Carolina. Douthitt (1915) described *C. p. americana* as a new variety from North America. Arnold (1938) followed Douthitt by retaining the variety as a valid sub-species.

6. *MONIEZIA EXPANSA (Rudolphi, 1805)

Host: *Odocoileus v. virginanus.*
Position: Intestine.

Identified from proglottids.

Sub-Family: LINSTOWIINAE Fuhrmann, 1907

7.* OOCHORISTICA MEPHITIS Skinker, 1935

Hosts: *Mephitis nigra, Urocyon c. cinereoargenteus.*
Position: Duodenum.

Common in the skunk (78%), *O. mephitis* was probably accidental in the fox. As many as 740 worms were found in a single skunk. Skinker (1935) reported it from skunks only. Hughes (1940) included it in his key to species of the genus. In most of the hosts, these forms clogged the gut so greatly that little or no free space was available. No other helminths were found in the same region of the host. 11 triradiate specimens were encountered.

Family: TAENIDAE Ludwig, 1886

8. TAENIA PISIFORMIS (Bloch, 1780) Gmelin, 1790

Host: *Urocyon c. cinereoargenteus.*
Position: Intestine.

As many as 31 specimens were found in a single gray fox. Hall (1919) has recorded it from this same host species. *T. pisiformis* was found commonly in local dogs and cats. A few lesions were observed.

9. CYSTICERCUS (TAENIA) PISIFORMIS

Hosts: *Sylvilagus f. transitionalis, Ondatra zibethica.*
Position: Liver, mesentery.

10. *SCHIZOTAENIA AMERICANA (Stiles, 1895) Janicki, 1906

Host: *Erethizon dorsatum.*
Position: Intestine.

431 specimens of *S. americana* were found in a single porcupine. Lesions and hemorrhagic areas were present. The lumen of the gut was clogged shut in the infected area.

Family: HYMENOLEPIDIDAE Railliet and Henry, 1909
Sub-Family: HYMENOLEPIDINAE Ransom, 1909

11. *HYMENOLEPIS EVAGINATA Barker and Andrews, 1915

Host: *Ondatra zibethica.*
Position: Intestine.

A single specimen of this tapeworm, described by Barker and Andrews in Barker (1915), was found in a muskrat.

12. HYMENOLEPIS sp.

Host: *Myotis l. lucifugus.*
Position: Intestine.

Family: MESOCESTOIDIDAE Fuhrman, 1907
Sub-Family: MESOCESTOIDINAE Luhe, 1894

13. *MESOCESTOIDES VARIABILIS Mueller, 1928

Host: *Procyon l. lotor.*
Position. Duodenum.

15 specimens of *M. variabilis*, from one of two raccoons, were recovered. Chandler (1942) reported it from raccoons in Texas. The present study offered evidence to support the conclusions of Chandler that the varieties *M. variabilis* established by Mueller (1928) are invalid.

Phylum: ACANTHOCEPHALA Rudolphi, 1808

1. *MONILIFORMIS CLARKII (Ward, 1917) Van Cleave, 1924

Host: *Mephitis nigra.*
Position: Duodenum.

One skunk had 18 specimens of *M. clarki* in the duodenum. Slight lesions, with minor hemorrhages, were evident. Chandler (1941) reviewed the genus *Moniliformis* and indicated that *M. clarki* had been found in *Sciurus, Citellus,* and *Scalopus,* in the midwestern states of North America. Peery (1941) recorded a case of peritoneal moniliformiasis in a fox squirrel.

2. "Acanthocephala"

Host: *Philohela minor.*
Position: Duodenum.

A single acanthocephalan, too badly disintegrated for identification was found in a woodcock.

Phylum: NEMATODA Rudolphi, 1808
Superfamily: ASCAROIDEA Railliet and Henry, 1915
Family: ASCARIADAE Baird, 1853
Sub-Family: ASCARINAE (Railliet and Henry, 1912) Travassos, 1913

1. *ASCARIS COLUMNARIS (Leidy, 1856)

Host: *Mephitis nigra.*
Position: Duodenum.

84% of the skunks examined were infected with this nematode. As many as 108 specimens were found in a single host. The intestines of freshly killed, infected skunks bulged and expanded with the worms present. Lesions were commonly observed. No other helminths were found in the same region of the gut. Occasionally, probably due to post-mortem migration, individual specimens were found in the stomach or in the lower gut.

2. TOXOCARA CANIS (Werner, 1782)

Hosts: *Urocyon c. cinereoargenteus, Vulpes fulva.*
Position: Duodenum.

Few specimens of this nematode were found in one of each of the hosts. *T. canis* was found commonly in local dogs.

Sub-Family: ASCARIDIINAE Travassos, 1919

3. *ASCARIDIA BONASAE Wehr, 1940

Host: *Bonasa u. umbellus.*
Position: Duodenum.

When first found, this nematode was believed to be *A. lineata* (Schreber, 1866). Wehr (1940) suggested that the *A. lineata* of various authors, reported from the grouse, is a separate species, and named it *A. bonasae*. Boughton (1937) and Fisher (1939) found it commonly in grouse in Minnesota and Michigan. In the present study, but few worms were found in the hosts infected.

4. ASCARIDIA GALLI (Schneider, 1866) Schwartz, 1925

Host: *Accipiter v. velox.*
Position: Duodenum.

This nematode, known commonly as *A. lineata,* a familiar poultry parasite, was probably accidental in the hawk.

Superfamily: STRONGYLOIDEA Weinland, 1858
Family: METASTRONGYLIDAE Leiper, 1908
Sub-Family: METASTRONGYLINAE Leiper, 1908

5. *CRENOSOMA VULPIS Zeder, 1800

Host: *Vulpes fulva.*
Position: Trachea and lungs.

In the one host infected with this nematode, the trachea and bronchioles were plugged, lesions and small hemorrhagic areas abundant. The trapper who collected this animal said it "appeared sickly in the trap."

6. *CRENOSOMA ZEDERI Goble, 1942

Host: *Mephitis nigra.*
Position: Trachea and bronchioles.

C. zederi, described by Goble (1942) from the skunk in New York, was found in 31% of the skunks examined. A few hemorrhagic areas, with bloody mucous clots in the bronchioles, were observed.

Family: ANCYLOSTOMIDAE (Looss, 1905) Lane, 1917
Sub-Family: NECATORINAE Lane, 1917

7. UCINARIA STENOCEPHALA (Railliet, 1884)

Hosts: *Urocyon c. cinereoargenteus, Vulpes fulva.*
Position: Duodenum.

All of the red foxes (*V. fulva*) examined were infected with this hookworm. No pathological conditions were found.

Family: TRICHOSTRONGYLIDAE Leiper, 1912
Sub-Family: TRICHOSTRONGYLINAE Leiper, 1908

8. OBELISCOIDES CUNICULI (Graybill, 1923) Graybill, 1924

Host: *Sylvilagus f. transitionalis.*
Position: Stomach.

A single specimen of this stomach worm was taken from one rabbit. *Alicata* (1932) described the life cycle.

Superfamily: OXYUROIDEA Railliet, 1916
Family: OXYURIDAE Cobbold, 1864
Sub-Family: OXYURINAE Hall, 1916

9. *PASSALURUS AMBIGUUS (Rudolphi, 1819) Dujardin, 1845

Host: *Sylvilagus f. transitionalis.*
Position: Cecum.

One rabbit harbored over 300 specimens of this worm.

Sub-Family: SYPHACIINAE Railliet, 1916

10. *WELLCOMIA EVOLUTA (Linstow, 1899)

Host: *Erethizon dorsatum.*
Position: Cecum.

Over 2150 specimens of this nematode were recovered from a single porcupine. The cecum was greatly distended, but no pathological conditions were observed. Canavan (1931) reported it from this same host species in Philadelphia, Penn.

Family: HETERAKIDAE Railliet and Henry, 1914
Sub-Family: HETERAKINAE Railliet and Henry, 1912

11. *HETERAKIS GALLINAE (Gmelin, 1790) Freeborn, 1923

Host: *Phasianus c. torquatus.*
Position: Cecum.

The only helminth collected from the pheasant, *H. gallinae* was found in 75% of these hosts examined. Madsen (1941) found it the most commonly occurring worm in pheasants in Denmark.

Superfamily: TRICHUROIDEA Railliet, 1916
Family: TRICHURIDAE Railliet, 1915
Sub-Family: CAPILLARIINAE Railliet, 1915

12. *CAPILLARIA AEROPHILA (Creplin, 1839)

Host: *Vulpes fulva.*
Position: Trachea and bronchi.

C. aerophila was found in two of the four red foxes examined. The left bronchus of one host was completely occluded by these worms. The economic importance of this nematode was indicated by Christenson (1935).

13. *CAPILLARIA PLICA (Rudolphi, 1819)

Hosts: *Vulpes fulva, Rattus norvegicus.*
Position: Bladder.

Few worms were recovered from infected hosts. The life cycle of *C. plica* was studied by Petrov and Borovkova (1942).

14. *CAPILLARIA sp.

Host: *Tamias striatus.*
Position: Intestine.

Too far disintegrated for specific identification.

Family: TRICHINELLIDAE Ward, 1907
Sub-Family: TRICHINELLINAE Ransom, 1911

15. *TRICHINELLA SPIRALIS (Owen, 1835) Railliet, 1895

Host: *Rattus norvegicus.*
Position: Diaphragm, tongue, muscles.

Two rats were infected so heavily with the larvae of this nematode that they were too sluggish to move rapidly. They were shot on the Amherst Garbage Dump. The economic importance of this worm is too well known to warrant discussion at this time. Cameron (1938), Hall and Collins (1937), and Sawitz (1938) indicate the prevalence and distribution of *Trichinella* in North America.

Superfamily: SPIRUROIDEA Railliet and Henry, 1915
Family: PHYSALOPTERIDAE Leiper, 1908
Sub-Family: PHYSALOPTERINAE Railliet, 1893

16 *PHYSALOPTERA MAXILLARIS Molin, 1860

Host: *Mephitis nigra.*
Position: Stomach.

100% of the skunks examined were heavily infected with this nematode. One host had as many as 517 in the stomach. Although there seemed little room for food, the skunk showed no external visible adverse condition.

17. *PHYSALOPTERA sp. Immature

Host: *Vulpes fulva.*
Position: Esophagus.

Summary

An examination of birds and mammals commonly found in Massachusetts was made for their helminth parasites. Nine species of birds (49 specimens) and 14 species of mammals (122 specimens) were studied. 40 species of helminths were obtained: 17 nematodes, 13 cestodes, eight trematodes, and two acanthocephalans. Most of the distribution records are new. Many of the parasites may be important economically as seen by actual damage to surrounding tissues.

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The Plankton of Bayou DeSiard. I.
Notes on the Cladocera*

Aaron Seamster

To date the Cladocera of a typical southern bayou have never been recorded. Although Herrick (1887) published a paper on the Cladocera of the Gulf of Mexico and the South, and Birge (1910) published notes on southern Cladocera, these authors mentioned as Louisiana localities only the areas around Lake Charles and New Orleans. By comparison the present paper represents a study made over a period of one year and is confined to observations relative to the seasonal prevalence of the species of Cladocera found in Bayou DeSiard, a northern Louisiana locality.

Collections were made with a number 20 plankton net, preserved in ten per cent formalin, and taken weekly from June 12, 1942, through June 7, 1943. Water temperatures were recorded, and monthly averages computed. Only a cursory examination of the fresh material was made, whereas the major study was carried out on the preserved forms. Temporary glycerine mounts were freely used for identification purposes. A few specimens were mounted permanently and remain in the author's collection for future reference.

Bayou DeSiard is a relatively quiet body of water which is rich in organic matter. The average annual temperature observed in this study was 21° C. (January 7.5° C. – August 32° C.). The conspicuous planktonic fauna and flora includes Cladocera, copepods, ostracods, rotifers, and algae.

There is insufficient evidence to indicate a pronounced seasonal variation of the cladoceran population in Bayou DeSiard, but it is worth while to note that some species appeared in collections over a period of several months and were then absent for varying lengths of time. For example, *Ilyocryptus spinifera* was found regularly in the August and September collections, but did not appear again until January. *Holopedium amazonicum* was observed only during April, May, and June with a large number of both adults and young present in the June collections. *Bosmina longirostris* was recorded during the first seven months of the year, January through July, but was absent until December. *Chydorus sphaericus* was found throughout the year. It was observed that the total number of cladocera reached a peak during the months of January and February. A corresponding minimum was noted during October and November. *Bosmina longirostris* was very numerous in the January and February collections; 100 cladocera counted at random in each of two samples for these months revealed 85% of the organisms to be *B. longirostris*.

* A Contribution from the Biological and Natural Science Department of Northeast Junior College of Louisiana State University.

The greatest variety of Cladocera was recorded in June when fourteen species were counted and in January when 9 different species were identified. (See Table 1.)

TABLE 1.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Bosmina longirostris	×	×	×	×	×	×	×					×
Bosmina longispina	×											
Euryalona occidentalis						×						
Ceriodaphnia rigaudi						×						
Pseudosida bidentata								×				
Alona affinis	×											
Alona guttata	×		×			×			×			×
Alona costata						×	×		×	×	×	
Diaphanosoma brachyurum				×		×						
Sida crystallina	×			×	×				×	×	×	×
Daphnia longispina		×	×	×	×	×						
Leydigia quadrangularis						×					×	
Pleuroxus hamulatus	×	×				×	×	×	×		×	
Ilyocryptus spinifera	×		×			×		×	×			
Macrothrix rosea						×		×				
Daphnia pulex		×			×	×	×			×		×
Holopedium amazonicum				×	×	×						
Ceriodaphnia quadrangula	×	×		×	×			×				
Chydorus sphaericus	×	×	×	×	×	×	×	×	×	×	×	×

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Possible Establishment of the Hamster in the United States

Charles A. Reed

The golden hamster of Syria (*Mesocricetus auratus*) was first introduced into the laboratories of the United States directly from Jerusalem in 1939 (personal communication from J. H. Bauer, International Health Division, Rockefeller Institute for Medical Research, New York City). Since then, this hamster has become a common laboratory animal throughout the country, and is used for a wide variety of purposes[1] and in addition is handled commercially by animal breeders and even by pet shops. From laboratories, hamsters radiate out as "pets" of students and animal keepers. Under such conditions, escape of a few animals now and then is inevitable, and has already happened several times, to my knowledge, in the regions of San Francisco bay and Portland, Oregon, and has undoubtedly happened elsewhere.[2]

It will be interesting to observe what success, if any, this exotic cricetine rodent has in establishing itself in the western hemisphere. As yet, to my knowledge, it has had no such success, and actually it may never have. Several factors are against it, other than the low initial population which would find itself, at any one time, in a position favorable for breeding. First, it is a slow and deliberate mouse, which does not have, in my opinion, the quick-witted intelligence of our native mice; and second, to date its known escapes have been mostly into metropolitan areas, where it has to compete with murine rats, whereas in its native habitat (around Aleppo, Syria) it is a country-dweller.

However, the golden hamster does have several factors in its favor, if it can once establish itself: its capacious cheekpouches, coupled with determined storage habits, insure it ample food supplies for times of scarcity (in fact, in parts of Europe, the depredations of the related *Cricetus* are so well-known that any person who hoards things is colloquially termed a "hamster"); the animal will, under natural conditions, burrow to the protective depth of 12 feet to establish a nest; individuals will survive at least 15 days without food or water with only a slight diminution of vigor (personal communication from T. C. Groody, formerly of the U. S. Public Health Service, San Francisco); and, in addition, the reproductive rate is fairly high, with litters of four to eight, and a gestation period of 16 days.

In spite of these adaptations for survival, in its native habitat the animal is restricted to a limited area and possibly it can never become established in the western hemisphere in competition with the fauna already present. If it does, it is anticipated that, at least in the United States, the coast of southern California would be most favorable for it, since the climatic conditions there most nearly duplicate the animal's natural habitat.

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1 Morton, Jour. Bacter. **45**:194, 1943.

2 A more general discussion of the golden hamster, for those unacquainted with it, may be found in Bruce and Hindle, Proc. Zool. Soc. London **1934**:361-366.

If the animal becomes established in California, the event will demonstrate the ineffectiveness of laws aimed at the exclusion of foreign mammals and birds. For the Wild Bird and Animal Importation Act of the State of California, Chapter 76, Statutes of 1933, Section 1, Regulation 1, absolutely denies importation of all hamsters into the state, and provides for the exportation or destruction of same when found. In addition, there was issued, at the same time, an illustrated publication of the California Department of Natural Resources, 1933, "Rules and Regulations governing the Importation of Wild Birds and Animals into the State of California. . . .", written by the late James Moffitt.[3] This pamphlet supposedly is in the hands of every border inspector of the State Department of Agriculture and of every member of the State Division of Fish and Game.

Nevertheless, the golden hamster is widespread throughout laboratories in California, and is also reared commercially by animal breeders and kept by individuals as pets. Few, if any, of such laboratories and individuals know of the provisions of the above-mentioned law, or are aware of the dangers to the local flora and fauna, and to agriculture, from the establishment of hamsters in the wild.

Actually, importations of the golden hamster into California have been accomplished, at least in part, by permit from the State Department of Agriculture. I quote from a letter by W. C. Jacobsen, of the Division of Plant Industry: "We have refused, as has the State Division of Fish and Game, many requests for approval of permits to import hamsters except for medical and biological laboratory research and development of biologics. In this particular type of instance, investigation has revealed that in almost all instances the hamsters that are trafficked in for scientific purposes are from known laboratory or breeding stocks generally in captivity for many years and come within the exception in the Wild Bird and Animal Importation Act that they are of a "normally domesticated" character. The restrictions on wild hamsters have not been changed. We are not aware of any illegal possession of hamsters. . . ."

The author, for one, was in illegal possession of hamsters for more than two years, while in residence at Berkeley, and in total ignorance of that illegality, as are undoubtedly scores of people through the state. Moreover, the "normally domesticated" status of hamsters is open to question. Can anyone imagine that these animals, if they establish themselves in the wild, will be less harmful because their immediate ancestors lived in cages for a few generations? One has only to remember that it was the "domestic" rabbit that was introduced into Australia.

It would be interesting to know what provisions other states have made for the exclusion of harmful foreign animals, and how well these are being observed.

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[3] Condor **46**:60-66, 1944.

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The Perennial Species of Urtica in the United States east of the Rocky Mountains

F. J. Hermann

In connection with the growing economic interest in the nettle, *Urtica*, as a source of chlorophyll, the Bureau of Plant Industry, Soils and Agricultural Engineering undertook a review of the United States species of the genus as a preliminary step in making field trials of such kinds as might be brought under cultivation in the eastern United States. The taxonomic work was initiated by Mrs. F. C. Weintraub who left before the data on the plants grown for observation could be obtained.

Preliminary horticultural studies by Dr. E. C. Stevenson, of the Division of Drug and Related Plants, on a number of selections from the Pacific Coast indicated that these species are not adapted to production in the eastern United States. The taxonomic problem thus became reduced to an attempt to find distinctions between the perennial nettles east of the Rocky Mountains, particularly between *U. dioica* L. and *U. procera* Muhl. which are the two nettles that have shown greatest promise as potential economic plants. The annuals, *U. urens* L. and *U. chamaedryoides* Pursh, are too small to have any practical value as sources of chlorophyll.

All the work upon this investigation completed by Mrs. Weintraub was repeated. This included: (1) a review of the pertinent literature upon the subject, such as Professor M. L. Fernald's treatment of the genus in Rhodora 28: 191-199 (1926), a manuscript key to the U. S. species of *Urtica* based upon material in the U. S. National Herbarium by Mr. C. V. Morton, "Indentification of Urtica" published by the Post Institute of New York (1943), and keys and descriptions in all the important floras of eastern and central U. S.; (2) a study of the material in the U. S. National Herbarium and the Herbarium of the U. S. National Arboretum, particular attention being given to the many collections cited by Professor Fernald; (3) field studies of wild plants at Sugar Loaf Mt. and along the Potomac River above Chain Bridge; and (4) studies of the extensive cultivated collections at Beltsville in the field and of herbarium specimens prepared from this material. The herbarium study was extended to include *U. dioica* and its variations in Europe and Asia. All of my observations and conclusions bore out those of Mrs. Weintraub, and the additional investigations undertaken resulted in the conviction that not merely have "too many" species of perennial nettles been recognized east of the Rockies, as she had concluded, but that we really have no more than a single species, with one or possibly two native varieties.

Discussion

In 1926 Fernald (l.c.) recognized three native perennial species of *Urtica* east of the Rocky Mountains, in addition to the supposedly introduced *U.*

dioica L. These were *U. procera* Muhl., *U. gracilis* Ait. and *U. viridis* Rybd. They were characterized as a group by the possession of stipules which were said to be 'scarious to herbaceous in texture and green to at most pale-brown"; whereas in their western relatives the stipules were said to be "subcoriaceous to coriaceous and soon becoming deep-brown to castaneous."

In maintaining these three plants as specifically distinct from *U. dioica*, Prof. Fernald admitted their lack of any diagnostic floral- or fruit-characters. The basis for his recognition of the segregates is expressed in the following quotation from his paper (l.c. 191): "*U. dioica* is, as its name implies, dioecious; the native American plants strongly tend to be monoecious. In the latter series wholly pistillate individuals frequently occur but in the whole range of native American plants studied I have found no specimens which have only staminate inflorescences; various mixtures occur but all American plants apparently have some of the terminal racemes pistillate. On this account and since the American plants have clearly defined and wholly characteristic and consistent ranges, I am treating them as species. . . ." With regard to the nonexistence of purely staminate plants among *U. procera, U. gracilis* and *U. viridis*, it may be stated that whereas the present study has indicated that such individuals appear to be very rare they do nevertheless occur, in fact the sheet in the U. S. National Herbarium of one of the collections cited by Fernald (A. Nelson 590, Mexican Mines, Wyo.) as "characteristic" *U. viridis* shows no trace of pistillate flowers. As to the "clearly defined and wholly characteristic and consistent ranges" of the American plants, the contradictory seems greatly to outweigh the supporting evidence for this.

The widespread and generally accepted belief that *U. dioica* is a rare species in the United States definitely appears to be erroneous, particularly with regard to the Mid-Atlantic States. It is the only nettle, for example, so far found in the District of Columbia area. All of the local material in the U. S. National Herbarium, representing collections from Takoma Park, Rosslyn, Chain Bridge, Glen Echo, Plummer's Island, banks of the B. and O. Canal, Hyattsville (Prince Georges Co., Md.)and Langley (Fairfax Co., Va.), and in the Herbarium of the National Arboretum, representing material from Antietam (Washington Co., Md.), Sugar Loaf Mt. (Frederick Co., Md.) and Chain Bridge (D. C.), is unmistakably *U. dioica*.

The characters generally relied upon for distinguishing the four perennial eastern nettles are well summed up in Mr. Morton's key (based principally upon Fernald's treatment) as follows:

Plants usually dioecious. Leaf blades broadly ovate, strongly covered with stinging hairs. European species, possibly casually introduced into the U. S., but if so certainly very rare ..... 1. *U. dioica.*

Plants monoecious. All native species.

Petioles 1/5 - 3/5 as long as the leaf blades; staminate inflorescences slender.

Leaves subtending the lowest inflorescences with an average of 25 pairs of teeth (range 19-38), averaging 11 cm. long (range 6.5 - 18 cm. long); petioles averaging 4.5 cm. long (range 1.5 - 8.5 cm.); stem pilose or pubescent above but with very few stinging hairs; leaf blades of a lanceolate type, usually not cordate at base ..... 2. *U. procera.*

Leaves subtending the lowest inflorescences with an average of 17 pairs of teeth (range 13 - 23), averaging 9 cm. long (range 5 - 15 cm.); petioles averaging 3 cm. long (range 1.5 - 5.5); stem usually with stinging hairs above, often lacking other pubescence; leaf blades usually of an ovate type, usually cordate at base ..... 3. *U. gracilis.*

Petioles 1/8 - 1/4 as long as leaf blades; staminate inflorescences thick. Leaf blades with an average of 17 pairs of teeth (range 11 - 25),, averaging 7 cm. long (range 3.5 - 10 cm.); petioles averaging 1.3 cm. long (range 0.7 - 2.5 cm.); stems glabrous or pilose above ..... 4. *U. viridis.*

Additional characteristics emphasized by Fernald and the ranges he ascribes to the plants are as follows:

U. procera: leaves usually cinereous-puberulent beneath; stipules cinereous-puberulent, much shorter than the petioles. N. S. and southern Que. to N. Dak., south to N. C. and La.

U. gracilis: leaves glabrous on both surfaces or sparingly pilose beneath; stipules glabrous or pilose, much shorter than the petioles. Northwestern Newfl. to n. Maine, western New England and northern N. Y.; Alberta and B. C., south to N. Mex. and Oregon.

U. viridis: leaves glabrous on both surfaces or pilose-hirsute beneath; stipules with glabrous scarious margins, from one-half as long to longer than the petioles. Straits of Belle Isle, Labrador southward along the coast to Lincoln Co., Maine; Alberta to S. Dak. and N. Mex.

It will be seen that the characters upon which the three native species are distinguished, in addition to being entirely vegetative, are quantitative rather than qualitative. Intermediates, as might be expected, are so frequent as to confute any attempt at sharp demarcation of one "species" from another, with the result that rarely do any two botanists employing these distinctions arrive at the same disposition for a given specimen, — particularly when the supposed geographic limitation of the entities is not taken into consideration. Fernald lays great stress upon geographic segregation, in fact must very often have rested his disposition of his cited specimens principally upon this to judge from the discrepancies of the material from the characters given in his descriptions. Mrs. Weintraub's conclusion from her comparison of herbarium material with these characters, that they "were found to be variable and . . . identification appeared to depend upon the idiosyncrasies of the taxonomist and to be a matter of personal discretion as to which were most important" and that "preconceived notions of geographical range have seemed to play their part also in determination of species," was amply borne out by my own studies. Field observations, moreover, showed that the alleged diagnostic characters, admittedly variable, were further influenced by season and by the age of the plants.

The unreliability of the purported distinctions between the native plants may perhaps best be illustrated from the following observations upon several of the extensive colonies of the plants grown in the field at Beltsville by Dr. Stevenson, since these data are taken not from a single plant, as is generally the case with herbarium specimens, but from a great many individuals. Numbers are those assigned to the field culture by Dr. Stevenson.

No. 48, from Plainfield, Wisc. and No. 49, from Dalton, Wisc. Petioles average 20 mm. in length, blades 75 mm. with 20 pairs of teeth, which should place them with *U. gracilis,* as should also the presence of stinging hairs and the lack of puberulence on the upper stem and the very sparsely puberulent stipules (which, however, are scarious-margined as in *viridis*). Yet Wisconsin does not lie within the range ascribed to *gracilis*. The principal affinity these specimens have with *procera* (which, from a geographic standpoint, they should be) is in the lanceolate, non-cordate leaves (except the lower which are strongly cordate).

No. 66, from Plymouth, Ind. *U. procera* according to leaf characters (petioles averaging 42 mm. long, blades 120 mm. with 22 pairs of teeth), but stems with stinging hairs above and no puberulence, leaves entirely glabrous beneath, and stipules glabrous.

No. 72A, from Middlebury, Ind. Again intermediate between *gracilis* (petioles averaging 27 mm., blades 95 mm. long; upper stem bristly with stinging hairs, otherwise glabrous; leaves glabrous beneath, the lower cordate; stipules glabrous), and *procera* (leaves with 25 pairs of teeth, those of the middle and upper stem lanceolate, not cordate) but in the summation of the characters closer to *gracilis* which would here be far from the range ascribed to it.

No. 92, from Windsor, Conn. In this the average length of petioles (44 mm.) and number of teeth (22 pairs) are those of *procera,* but the average blade-length (85 mm.) is that of *gracilis*. The narrowly oblong-lanceolate, non-cordate leaf blades of the mid-stem are decidedly *procera* in outline, yet the uppermost blades, as well as those on the lower part of the stem and basal shoots, are ovate and cordate. The bristly, non-puberulent upper stem, and the lack of pubescence on the lower leaf surfaces and on the stipules are additional characteristics of the supposedly northern and western *gracilis*.

No. 96, from Marion, Ohio. Outline and base of leaves those of *procera,* also length of petiole and blade (averages 40 mm. and 112 mm. respectively), but teeth (average 18 pairs) and glabrous lower leaf surfaces, upper stem and stipules of *gracilis*.

Unnumbered culture from Bevan, N. J. Leaf shape and base of *procera* but measurements (petioles averaging 35 mm., blades 85 mm., teeth 20 pairs) those of *gracilis,* and upper stem with an abundance of stinging hairs. Stipules densely puberulent (*procera*) on Aug. 1, glabrous (*gracilis*) by Oct. 15. In the early part of the season (up to mid-August) this colony had stems and branches as densely hispid with stinging hairs as the most characteristic *dioica,* some stinging hairs even being present on the upper leaf-surfaces, but showed no other tendencies of that plant.

Although transitional forms between *U. dioica* and the *procera-gracilis* complex are much less common than those between *procera* and *gracilis* and those between *viridis* and *gracilis* (the latter so prevalent that the anomalous bilateral range ascribed to *viridis* appears to be its only tangible characteristic), they do occur with sufficient frequency to cause difficulty in identification. This

is particularly true in the case of a herbarium specimen consisting of a pistillate plant only, since purely pistillate individuals are not at all rare in *procera* or *gracilis*, or even in the case of a series of specimens from an extensive pistillate clone or a series collected after the staminate inflorescences have disappeared. An instance of this may be illustrated by the colony of *Urtica* at the western base of Sugarloaf Mt., near Dickerson, Frederick County, Maryland. The general appearance of the plants in this colony suggested the *procera-gracilis* complex (in fact specimens from this source had been named *U. gracilis* by one botanist, and *U. procera* by another), the leaf-blades being not at all broadly ovate and their upper surfaces having very few stinging hairs. Although no staminate inflorescences could be found at the time this locality was visited (July 14), it was suspected that either the colony consisted of a single pistillate clone or that the staminate inflorescences had withered away by this date. Detailed study of a series of specimens from the colony, however, showed that they had more in common with *U. dioica*, although with marked *gracilis* tendencies.

Conclusions

Studies of the perennial nettles of eastern North America in the herbarium and under cultivation in the field suggest that we have but one species of *Urtica—U. dioica* L. The typical form of this may have been introduced from Europe, although the evidence now on hand does not seem to be sufficiently conclusive to warrant a decision either that it is or is not native.

Urtica dioica is not always well marked off from the nettles which have been called *U. gracilis* Ait., *U. viridis* Rydb. and *U. procera* Muhl., although supplementary characters helpful in distinguishing it from those plants were revealed by this study and are included in the key given below. For this reason, and because of the inconstancy of the alleged differences between *procra, gracilis* and *viridis* and the predominance of intermediates between these supposed entities, I prefer to follow Weddell (Monographie de la Famille des Urticées, 78, 1856) in uniting the latter three plants as *U. dioica* var. *procera* (Muhl.) Wedd. The differences between *procera, gracilis* and *viridis* appear to be tendencies only, and certainly those ascribed to Rydberg's *U. viridis* are so chimerical that I would not hesitate to reduce it outright to the synonymy of *U. gracilis*. It may be that more exhaustive studies of *U. gracilis*, embracing all the available material of it and of *U. procera*, would indicate that it merited rank as a variety of *U. dioica* parallel with var. *procera*, but if so the demarcation will have to be finely drawn and difficult at best, and obviously it does not show the well-marked geographic segregation commonly assigned to it.

It may be remarked that a review of the European and Asiatic material of *Urtica dioica* in the U. S. National Herbarium reveals that it includes a series of variations quite closely paralleling *U. procera, U. gracilis* and *U. viridis* as well as additional forms not met with in America. Several of these variants are given nomenclatorial recognition by some authors as varieties of *U. dioica*, but they are not commonly set up as species in those countries. Furthermore, the reduction of the *procera-gracilis* complex to subordinate rank is more in accord with the disposition of similar variations in related genera. The well-marked

var. *drummondiana* Wedd. of *Boehmeria cylindrica* (L.) Sw., for example, is much more distinct from typical *B. cylindrica* than is *Urtica gracilis* from *U. procera*.

KEY

Plants dioecious. Leaf-blades usually broadly ovate and cordate at base, usually strongly hispid with stinging hairs on both surfaces, the lower surface generally also pilose with long, ascending, straight, firm hairs, *the teeth 3 - 11 mm. deep* (*averaging* 5 - 6 mm.); stem pilose and strongly hispid with stinging hairs above, the nodes with dense clusters of stinging bristles below the stipules; stipules puberulent and usually conspicuously ciliate especially toward the apex ....*Urtica dioica* L.

Plants usually monoecious (pistillate plants occasional, but entirely staminate plants rare). Leaf-blades oblong-lanceolate to ovate, tapering or rounded to cordate at the base, the upper surface usually glabrous, the lower surface glabrous or pubescent with either short appressed or erect but very tenuous, weak hairs, *the teeth 1 - 5 mm. deep* (*averaging 2 - 3.5 mm.*); stem glabrous, puberulent, or moderately (occasionally strongly) hispid with stinging hairs above, the clusters of bristles at the nodes generally short and inconspicuous; stipules glabrous to puberulent, rarely markedly ciliate .....*Urtica dioica* var. *procera* (Muhl.) Wedd. (including *U. procera* Muhl., *U. gracilis* Ait. and *U. viridis* Rydb.)

DIVISION OF PLANT EXPLORATION AND INTRODUCTION,
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A Contribution to our Knowledge of the Wild and Cultivated Flora of Ohio—II

Harold N. Moldenke

The present contribution comprises an annotated list of 333 collections of Ohio plants additional to the 2734 recorded in the first paper in this series,[1] representing 179 different identified species and varieties in 121 genera and 65 families. The sequence of families is the same as that followed in the first paper, and as in the case of that paper, most of the records of this contribution are based on material found on or very near to the land owned or leased by the North Appalachian Experimental Watershed, near Fresno, Chili, and Canal Lewisville, Coshocton County, Ohio. This locality is abbreviated to "N. A. E. W." on the following pages. Vouchers for most of the records of this list are deposited in the herbarium of the North Appalachian Experimental Watershed, the herbarium of Earlham College, and the herbaria of the institutions with which the specialists who have examined them are connected.

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Chroococcaceae

Anacystis rupestris (Lyngb.) Drouet and Daily—Coshocton Co.: associated with *Nostoc microscopicum* scraped from rock-ledges at Butternut Falls, N. A. E. W., *King 1027*, in part, det Drouet, *King 1037*, det. Drouet.

Oscillatoriaceae

Lyngbya aestuarii Gom.—Coshocton Co.: associated with *Schizothrix stricklandii* on moist soil in ditch near Station, N. A. E. W., *King 858*, in part, det. Drouet; associated with *Nostoc muscorum* on soil of Lautenschlager farm, Little Mill Creek area, N. A. E. W., *King 865*, in part, det. Drouet.

Lyngbya sp. nov.?—Coshocton Co.: scraped from rocks under falling water at Butternut Falls, N. A. E. W., *King 1004*, det. Drouet.

Microcoleus vaginatus Gom.—Coshocton Co.: on moist soil bottom of ditch near Station, N. A. E. W., *King 1049*, det. Drouet; on clod in corn mulch plot D-8, subsurface tilled, N. A. E. W., *King 863*, det. Drouet; in about ½ inch of water in roadside ditch near mine, N. A. E. W., *King 978*, det. Drouet, "specimen having unitrichomatiferous filaments"; associated with *Anabaena oscillarioides* in puddle in roadway near Station, N. A. E. W., *King 1002*, in part, det. Drouet, "specimen with

1 Castanea 9:1-80. 1944.

phormidioid growth form"; in shallow water of roadside ditch near Station, N. A. E. W., *King 1015*, det. Drouet, "chiefly phormidioid growth"; associated with *Anabaena oscillarioides* near Station, N. A. E. W., *King 1017*, in part, det. Drouet, "specimen having unitrichomatiferous filaments"; on soil near Station, N. A. E. W., *King 1055*, det. Drouet.

Oscillatoria brevis Gom.—Coshocton Co.: in puddle in roadway near Station, N. A. E. W., *King 1011*, det. Drouet.

Oscillatoria limosa Gom.—Coshocton Co.: in shallow water near Station, N. A. E. W., *King 869*, det. Drouet, *King 870*, det. Drouet; at gauging station no. 9, Little Mill Creek watershed, N. A. E. W., *King 1030*, det. Drouet.

Phormidium subfuscum var. *joannianum* Gom.—Coshocton Co.: scraped from rocks under falling water at Butternut Falls, N. A. E. W., *King 1021*, det. Drouet; *King 1022*, det. Drouet.

Phormidium uncinatum Gom.—Coshocton Co.: associated with *Symploca muscorum* on low flow-spillway of flume 177, N. A. E. W., *King 996*, in part, det. Drouet; in running water on main spillway of flume 177, N. A. E. W., *King 1008*, det. Drouet; on bottom of concrete roadside channel by flume 107, N. A. E. W., *King 1042*, det. Drouet, *King 1047*, det. Drouet.

Schizothrix friesii Gom.—Coshocton Co.: on soil of roadside ditch near Station, N. A. E. W., *King 849*, det. Drouet.

Schizothrix stricklandii Drouet—Coshocton Co.: associated with *Lyngbya aestuarii* on moist soil in ditch near Station, N. A. E. W., *King 858*, in part, det. Drouet.

Symploca kieneri Drouet—Coshocton Co.: on soil in open field near Lautenschlager farm, Little Mill Creek area, N. A. E. W., *King 857*, det. Drouet.

Symploca muscorum Gom.—Coshocton Co.: among moss on limb by edge of stream, Lautenschlager farm, Little Mill Creek area, N. A. E. W., *King 860*, det. Drouet; associated with *Phormidium uncinatum* on low-flow spillway of flume 177, N. A. E. W., *King 996*, in part, det. Drouet.

STIGONEMATACEAE

Fischerella ambigua (B. & F.) Gom.—Coshocton Co.: on bare soil areas of open hillside pasture, Lautenschlager farm, Little Mill Creek area, N. A. E. W., *King 851*, det. Drouet; *King 852*, det. Drouet; on rough eroded soil at base of tree along stream, Lautenschlager farm, Little Mill Creek area, N. A. E. W., *King 866*, det. Drouet.

NOSTOCACEAE

Anabaena oscillarioides B. & F.—Coshocton Co.: associated with *Microcoleus vaginatus* in puddles in roadway near Station, N. A. E. W., *King 1002*, in part, det. Drouet; *King 1017*, in part, det. Drouet.

Anabaena variabilis B. & F.—Coshocton Co.: on soil near Station, N. A. E. W., *King 1024*, det. Drouet; in ditch along Fresno road, N. A. E. W., *King 1026*, det. Drouet.

Cylindrospermum licheniforme B. & F.—Coshocton Co.: on wet soil in roadside ditches, N. A. E. W., *King 1034*, det. Drouet.

Cylindrospermum majus B. & F.—Coshocton Co.: on soil near Station, N. A. E. W., *King 864*, det. Drouet.

Cylindrospermum muscicola B. & F.—Coshocton Co.: on open soil areas in meadow in watershed 109, N. A. E. W., *King 852*, det. Drouet; on moist clay in shady area, Lautenschlager farm, Little Mill Creek area, N. A. E. W., *King 859*, det. Drouet; on soil near Station, N. A. E. W., *King 1023*, det. Drouet.

Nostoc microscopicum B. & F.—Coshocton Co.: among mosses on rock-ledge at Butternut Falls, N. A. E. W., *King 1020*, det. Drouet; associated with *Anacystis rupestris* scraped from rock-ledges at Butternut Falls, N. A. E. W., *King 1027*, in part, det. Drouet.

Nostoc muscorum B. & F.—Coshocton Co.: associated with *Lyngbya aestuarii* on soil of Lautenschlager farm, Little Mill Creek area, N. A. E. W., *King 865*, in part, det. Drouet.

CERATIOMYXACEAE

Ceratiomyxa fruticulosa (O. F. Muell.) T. H. Macbr.—Coshocton Co.: on dead wood in forest near Station, N. A. E. W., *King 1181*, det. Hagelstein; whitish mass on wood in forest southwest of tower, N. A. E. W., *King 1210*, det. Hagelstein; on dead wood in forest southwest of tower, N. A. E. W., *King 1212*, det. Hagelstein, *King 1227*, det. Hagelstein; *King 1233*, det. Hagelstein; *King 1257*, det. Hagelstein; on rotten wood, Lower Spoon Creek, N. A. E. W., *King 1335*, det. Hagelstein.

Ceratiomyxa fruticulosa var. *flexuosa* A. Lister—Coshocton Co.: very abundant on underside of loose bark on logs in woodpile on CCC camp ground, N. A. E. W., *King 1102*, det. Hagelstein.

Ceratiomyxa fruticulosa var. *porioides* (Alb. & Schwein.) A. Lister—Coshocton Co.: white sticky mass on wood in woodpile on CCC camp ground, N. A. E. W. *King 1092*, det. Hagelstein.

CRIBRARIACEAE

Cribraria violacea Rex—Coshocton Co.: associated with *Physarum wingatense* on wood in forest southwest of tower, N. A. E. W., *King 1202*, in part, det. Hagelstein.

Cribraria sp.—Coshocton Co.: on wood, Lower Spoon Creek, N. A. E. W., *King 1327*, det. Hagelstein.

STEMONITACEAE

Stemonitis axifera (Bull.) T. H. Macbr.—Coshocton Co.: on dead wood in forest southwest of tower, N. A. E. W., *King 1193*, det. Hagelstein.

Stemonitis fusca Roth—Coshocton Co.: on dead wood in forest southwest of tower, N. A. E. W., *King 1225*, det. Hagelstein.

Stemonitis herbatica Peck—Coshocton Co.: on dead wood in forest southwest of tower, N. A. E. W., *King 1218*, det. Hagelstein.

Stemonitis splendens Rost.—Coshocton Co.: on wood near Station, N. A. E. W., *King 1186*, det. Hagelstein.

PHYSARACEAE

Fuligo septica (L.) Weber—Coshocton Co.: on wood in forest near tower, N. A. E. W., *King 1261*, det. Hagelstein; on wood in forest near Station, N. A. E. W., *King 1331*, det. Hagelstein.

Leocarpus fragilis (Dickson) Rost.—Coshocton Co.: pyriform fruiting-bodies trailing along on leaf of *Fagus grandifolia* from forest litter in picnic woods, watershed 177, N. A. E. W., *King 1190*, det. Hagelstein.

Physarum nutans Pers.—Coshocton Co.: on dead wood in forest southwest of tower, N. A. E. W., *King 1226*, det. Hagelstein; on dead limb in forest litter of woods near Butternut Falls, N. A. E. W., *King 1373*, det. Hagelstein.

Physarum viride (Bull.) Pers.—Coshocton Co.: yellow-stalked structures on dead wood in forest southwest of tower, N. A. E. W., *King 1199*, det. Hagelstein.

Physarum wingatense T. H. Macbr.—Coshocton Co.: among mosses on log in woods near mine, N. A. E. W., *King 1184*, det. Hagelstein; on dead wood in forest southwest of tower, N. A. E. W., *King 1201*, det. Hagelstein; *King 1230*, det. Hagelstein; *King 1234*, det. Hagelstein; associated with *Cribraria violacea* on wood in forest southwest of tower, N. A. E. W., *King 1202*, in part, det. Hagelstein.

DIDYMIACEAE

Diachea bulbillosa (Berk. & Br.) A. Lister—Coshocton Co.: on leaves in forest litter in woods southwest of tower, N. A. E. W., *King 1206*, det. Hagelstein.

Mucilago spongiosa (Leyss.) Morg.—Coshocton Co.: white nearly cylindrical masses growing on stems of plants in woods near Station, N. A. E. W., *King 1372*, det. Hagelstein.

ARCYRIACEAE

Arcyria cinerea (Bull.) Pers.—Coshocton Co.: associated with *Hemitrichia vesparium* on wood in forest southwest of tower, N. A. E. W., *King 1221*, in part, det. Hagelstein; in woods southwest of tower, N. A. E. W., *King 1231*, det. Hagelstein.

Arcyria cinera var. *digitata* (Schwein.) G. Lister—Coshocton Co.: on dead wood in forest southwest of tower, N. A. E. W., *King 1374*, det. Hagelstein.

Arcyria denudata (L.) Wettst.—Coshocton Co.: on wood in woodpile, N.A.E.W., *King 1097*, det. Hagelstein; on wood in forest southwest of tower, N. A. E. W., *King 1219*, det. Hagelstein; on wood in forest near tower, N. A. E. W., *King 1258*, det. Hagelstein.

Arcyria pomiformis (Lars.) Rost.—Coshocton Co.: yellow growth on wood in forest southwest of tower, N. A. E. W., *King 1203*, det. Hagelstein.

TRICHIACEAE

Hemitrichia clavata (Pers.) Rost.—Coshocton Co.: on soft rotten wood on underside of log of *Fagus grandifolia*, N. A. E. W., *King 1095*, det. Hagelstein; on wood in woodpile, N. A. E. W., *King 1091*, det. Hagelstein; on damp wood in forest southwest of tower, N. A. E. W., *King 1234*, det. Hagelstein; on wood in forest near tower, N. A. E. W., *King 1253*, det. Hagelstein.

Hemitrichia serpula (Scop.) Rost.—Coshocton Co.: on leafmold in forest litter, woods southwest of tower, N. A. E. W., *King 1205a*, det. Hagelstein.

Hemitrichia vesparium (Batsch) T. H. Macbr.—Coshocton Co.: on wood in woodpile on CCC camp ground, N. A. E. W., *King 1100*, det. Hagelstein; associated with *Arcyria cinerea* on wood in forest southwest of tower, N. A. E. W., *King 1221*, in part, det. Hagelstein; on rotten wood, N. A. E. W., *King 1250*, det. Hagelstein; under bark of log in woodpile at Butternut Falls, N. A. E. W., *King 1371*, det. Hagelstein.

Trichia affinis de Bary—Coshocton Co.: on wood in woodpile, N. A. E. W., *King 1101*, det. Hagelstein; on rotten wood in forest southwest of tower, N. A. E. W., *King 1220*, det. Hagelstein.

TETRASPORACEAE

Gloeocystis vesiculosa Näg.—Coshocton Co.: scraped from moist rock in roadside ditch in watershed 119, N. A. E. W., *King 1041*, det. Drouet.

Tetraspora gelatinosa (Vauch.) Desv.—Coshocton Co.: very abundant in brook on hillside near watershed 130, N. A. E. W., *King 1039*, det. Drouet.

CHLOROCOCCACEAE

Chlorococcum humicola (Näg.) Rabenh.—Coshocton Co.: scraped from stone wall by spring in CCC camp ground, N. A. E. W., *King 1016*, det. Drouet; *King 1017*, det. Drouet, "specimen parasitized".

PROTOSIPHONACEAE

Protosiphon botryoides (Kütz.) Klebs—Coshocton Co.: associated with moss protonema on mud behind flume 177, N. A. E. W., *King 846*, det. Drouet.

ULOTRICHACEAE

Stichococcus subtilis (Kütz.) Klerck.—Coshocton Co.: on soil in roadside ditch near Station, N. A. E. W., *King 867*, det. Drouet; on soil near Station, N. A. E. W., *King 868*, det. Drouet.

Ulothrix sp.—Coshocton Co.: attached to limestone in shallow stream in watershed 119, N. A. E. W., *King 1051*, det. Drouet; *King 1052*, det. Drouet.

CHAETOPHORACEAE

Draparnaldia acuta (Ag.) Kütz.—Coshocton Co.: near the Station, N. A. E. W., *King 994*, det. Drouet.

Stigeoclonium sp.—Coshocton Co.: in roadside ditch near the Station, N. A. E. W., *King 1044*, det. Drouet; *King 1045*, det. Drouet.

TRENTEPOHLIACEAE

Trentepohlia aurea (L.) Mart.—Coshocton Co.: in little stream from coal mine near the tower, N. A. E. W., *King 768*, det. Drouet; *King 772*, det. Drouet.

TRIBONEMACEAE

Tribonema bombycina (Ag.) Derb. & Sol.—Coshocton Co.: in shallow water in roadside ditch, N. A. E. W., *King 1001*, det. Drouet; in shallow water near Station, N. A. E. W., *King 1003*, det. Drouet; in shallow water among rushes in marshy area near flume 177, N. A. E. W., *King 1010*, det. Drouet; *King 1012*, det. Drouet; *King 1029*, det. Drouet.

BOTRYDIACEAE

Botrydium granulatum (L.) Grev.—Coshocton Co.: on moist soil between grass clumps on Lautenschlager farm, Little Mill Creek area, N. A. E. W., *King 861*, det. Drouet, "specimen in palmelloid condition".

DESMIDIACEAE

Closterium sp.—Coshocton Co.: associated with *Mougeotia* in marsh above Butternut Falls, N. A. E. W., *King 1058*, in part, det. Drouet.

Cosmarium sp.—Coshocton Co.: on mud near flume 177, N. A. E. W., *King 1014*, det. Drouet.

Docidium sp.—Coshocton Co.: associated with *Zygnema* in roadside ditch near Station, N. A. E. W., *King 993*, det. Drouet.

ZYGNEMATACEAE

Mougeotia sp.—Coshocton Co.: associated with *Closterium* in marsh above Butternut Falls, N. A. E. W., *King 1058*, in part, det. Drouet.

HELMINTHOCLADACEAE

Batrachospermum sp.—Coshocton Co.: growing in dense tufts in spring in picnic woods, N. A. E. W., *King 995*, verif. Palmer.

MUCORACEAE

Pilobolus sp.—Coshocton Co.: sporangia attached to stems of *Juncus* in meadow near lysimeter 103, N. A. E. W., *King 1440*, det. Kern.

ERYSIPHACEAE

Erysiphe cichoracearum P. DC.—Coshocton Co.: on leaves of *Plantago rugelii* in meadow near watershed 123, N. A. E. W., *King 1416*, det. Stevenson; on leaves of *Cucurbita pepo* in corn field on Eberwine farm, N. A. E. W., *King 1417*, det. Stevenson; on leaves of *Verbena* in swamp area, N. A. E. W., *King 1430*, det. with a question by Stevenson.

Microsphaera alni (P. DC.) Wint.—Coshocton Co.: N. A. E. W., *King 1426*, det. Stevenson; *King 1429*, det. Stevenson.

Oidium curtisii (Berk.) Linder—Coshocton Co.: on loose rotten bark in log pile on CCC camp ground, N. A. E. W., *King 1090*, det. Linder; *King 1098*, det. Linder; *King 1103*, det. Linder.

MOLLISIACEAE

Orbilia coccinella (Sommerf.) P. Karst.—Coshocton Co.: on loose rotten bark in log pile on CCC camp ground, N. A. E. W., *King 1098a*, det. Linder.

Pseudopeziza medicaginis (Lib.) Sacc.—Coshocton Co.: on young plants of *Medicago sativa* growing in corn plots near watershed 130, N. A. E. W., *King 1386*, det. Kern.

MYCOSPHAERELLACEAE

Mycosphaerella rubi Roark—Coshocton Co.: associated with *Kuehneola uredinis* on underside of leaves of *Rubus allegheniensis* near Station, N. A. E. W., *King 1412*, in part, det. Kern.

GNOMONIACEAE

Gnomonia caryae (Ell. & Dearn.) Wolf—Coshocton Co.: spots resembling this species on leaves of *Carya ovata* in picnic woods near CCC camp, N. A. E. W., *King 1437*, det. Kern.

Gnomonia ulmea (Schwein.) Thüm.—Coshocton Co.: on leaves of *Ulmus fulva* from tree in watershed 177, N. A. E. W., *King 1421*, det. as "*Gnomia ulmea* (Schwein.) Thüm." by Kern.

PUCCINIACEAE

Kuehneola uredinis (Link) Arth.—Coshocton Co.: associated with *Mycosphaerella rubi* on underside of leaves of *Rubus allegheniensis* near Station, N. A. E. W., *King 1412*, in part, det. Kern.

Puccinia coronata Corda—Coshocton Co.: on stubble of *Avena sativa* on mulch plots of block C near lysimeter 103, N. A. E. W., *King 1387*, det. Kern.

Puccinia graminis var. *phlei-pratensis* (E. & H.) Stak. & Piem.—Coshocton Co.: associated with *Alternaria* and *Helminthosporium* on autumnal leaves of *Phleum pratense* in meadow back of carpenter shop, N. A. E. W., *King 1404*, in part, det. Kern.

Puccinia xanthii Schwein.—Coshocton Co.: wart-like growths on leaves of *Xanthium pensylvanicum* near Browning's barn, N. A. E. W., *King 1439*, det. Kern.

COLEOSPORIACEAE..

Coleosporium solidaginis (Schwein.) Thüm.—Coshocton Co.: on lower leaves of *Solidago juncea* in fields near watershed 115, N. A. E. W., *King 1402*, det. Kern; on lower leaves of *Solidago canadensis* var. *gilvocanescens* near watershed 115, N. A. E. W., *King 1403*, det. Kern; on underside of leaves of *Solidago* in meadow north of tower, N. A. E. W., *King 1424*, det. Kern; on leaves of *Erigeron* and *Aster* in meadow near lysimeter 103, N. A. E. W., *King 1435*, det. Kern.

MELAMPSORACEAE

Melampsora abietis-canadensis C. A. Ludwig—Coshocton Co.: on underside of leaves of *Populus grandidentata* from young trees in picnic woods near CCC camp, N. A. E. W., *King 1438*, det. Kern.

Pucciniastrum agrimoniae (Schwein.) Tranz.—Coshocton Co.: on lower yellowed leaves of *Agrimonia* near watershed 123, N. A. E. W., *King 1405*, det. Kern.

TREMELLACEAE

Exidia recisa Ditm.—Coshocton Co.: black oozy slime on dead log in woods, N. A. E. W., *Moldenke 14302*, det. with a question by Linder.

SPHAERIOIDEACEAE

Phyllosticta acericola Peck—Coshocton Co.: forming leaf-spots on leaves of *Rufacer rubrum* in woods west of field warehouse, N. A. E. W., *King 1431*, det. Kern.

Phyllosticta smilacina (Peck) Dearn.—Coshocton Co.: growing in insect lesions on leaves of *Smilax rotundifolia* var. *quadrangularis* at edge of woods near watershed 115, *King 1418*, det. Kern.

PHOMACEAE

Septoria plantaginis (Cas.) Sacc.—Coshocton Co.: on leaves of *Plantago lanceolata* along road to lysimeter 103, N. A. E. W., *King 1433*, det. with a question by Kern.

MELAMCONIACEAE

Colletotrichum cereale Manns—Coshocton Co.: lesions on leaves of *Poa pratensis* in meadow behind carpenter shop, N. A. E. W., *King 1406*, det. Kern.

Colletotrichum sp.—Coshocton Co.: associated with *Helminthosporium* on leaves of *Dactylis glomerata* in field near carpenter shop, N. A. E. W., *King 1432*, in part, det. Kern.

Gleosporium sassafras Ell. & Ev.—Coshocton Co.: growing in insect lesions on leaves of *Sassafras albidum* in woods west of field warehouse, N. A. E. W., *King 1428*, det. Kern.

MUCEDINACEAE

Pellicularia sp.—Coshocton Co.: N. A. E. W., *King 1384*, det. Stevenson, who says "Should be studied further."

Sepedonium chrysospermum E. Fries—Coshocton Co.: on *Boletus*, N. A. E. W., *King 1380*, det. Stevenson; N. A. E. W., *King 1381*, det. Stevenson; *King 1382*, det. Stevenson; *King 1382a*, det. Stevenson.

MONILIACEAE

Botrytis cinerea Pers.—Coshocton Co.: on leaves of *Impatiens* in leaf litter, N. A. E. W., *King 1352*, det. by Stevenson as "*Botrytis* sp. cf. *B. cinerea* Pers."; on fruit of *Rubus allegheniensis* in fields, N. A. E. W., *King 1379*, det. Stevenson.

DEMATIACEAE

Alternaria sp.—Coshocton Co.: associated with *Puccinia graminis* var. *phlei-pratensis* and *Helminthosporium* on autumnal leaves of *Phleum pratense* in meadow back of carpenter shop, N. A. E. W., *King 1404*, in part, det. Kern.

Cercospora barbareae Sacc.—Coshocton Co.: forming large yellow lesions on leaves of *Campe barbarea* in watershed 177, very widespread on basal rosettes, N. A. E. W., *King 1422*, det. Kern.

Cladosporium herbarum Link—Coshocton Co.: on polypore, N. A. E. W., *King 1377*, det. by Stevenson as "*Cladosporium* sp. of *C. herbarum* complex"; on sticking-tape from instrument shelter house, N. A. E. W., *King 1378*, det. Stevenson.

Fusella sp.—Coshocton Co.: near Station, N. A. E. W., *King 1351*, det. with a question by Stevenson.

Gonatobotryum maculicolum (Wint.) Sacc.—Coshocton Co.: in lesions of leaves of *Hamamelis virginiana* in woods north of tower, N. A. E. W., *King 1425*, det. Kern.

Helminthosporium sp.—Coshocton Co.: associated with *Puccinia graminis* var. *phlei-pratensis* and *Alternaria* on autumnal leaves of *Phleum pratense* in meadow back of carpenter shop, N. A. E. W., *King 1404*, in part, det. Kern; associated with *Colletotrichum* on leaves of *Dactylis glomerata* in field near carpenter shop, N. A. E. W., *King 1432*, in part, det. Kern.

DIPLOSCHISTACEAE

Diploschistes scruposus (Schreb.) Norm.—Coshocton Co.: growing in crusts on sandstone rocks in open fields, N. A. E. W., *King 957*, det. Nearing; *King 958*, det. Nearing; near Station, N. A. E. W., *King 963*, det. Nearing; *King 1057a*, det Nearing.

COLLEMATACEAE

Leptogium tremelloides (L.) S. F. Gray—Coshocton Co.: near Station, N. A. E. W., *King 930*, det. Nearing.

LECIDEACEAE

Lecidea platycarpa Ach.—Coshocton Co.: on sandstone rocks, N. A. E. W., *King 942*, det. Nearing.

Rhizocarpon concentricum (Davies) Beltr.—Coshocton Co.: on sandstone rocks, N. A. E. W., *King 941*, det. Nearing, who says "an unusual form, and I am not quite sure of the determination."

CLADONIACEAE

Cladonia chlorophaea (Floerke) Spreng.—Coshocton Co.: growing with *Leptogium tremelloides* near Station, N. A. E. W., *King 932*, det. Nearing.

Cladonia coniocraea (Floerke) Spreng.—Coshocton Co.: on exposed root of *Fagus grandifolia* above ravine, N. A. E. W. *King 911*, det. Nearing; among mosses on soil of watershed 196, N. A. E. W., *King 929*, det. Nearing; among mosses and liverworts on stones in woods, N. A. E. W., *King 939*, det. Nearing; associated with *Parmelia rudecta*, *Physcia endochrysea*, and *Physcia sorediata*, N. A. E. W., *King 1059*, in part, det. Nearing; near Station, N. A. E. W., *King 1057*, det. Nearing; *King 1062*, det. Nearing.

Cladonia squamosa (Scop.) Hoffm.—Coshocton Co.: growing in crusts on sandstone rocks in open fields, N. A. E. W., *King 957a*, det. Nearing.

Cladonia sp.—Coshocton Co.: on bark at base of *Fagus grandifolia* tree in ravine north of Station, N. A. E. W., *King 903a*, det. Nearing; near Station, N. A. E. W., *King 1064*, det. Nearing.

PARMELIACEAE

Parmelia aurulenta Tuck.—Coshocton Co.: on base of *Fagus grandifolia* tree above ravine, N. A. E. W., *King 919*, det. Nearing; near Station, N. A. E. W., *King 1062a*, det. Nearing.

Parmelia rudecta Ach.—Coshocton Co.: associated with *Cladonia coniocraea*, *Physcia endochrysea*, and *P. sorediata*, N. A. E. W., *King 1059*, in part, det. Nearing; near Station, N. E. A. W., *King 1088*, det. Nearing.

Parmelia saxatilis (L.) Ach.—Coshocton Co.: associated with *Physcia tribacia* near Station, N. A. E. W., *King 948*, det. Nearing.

PHYSCIACEAE

Physcia endochrysea (Hampe) Nyl.—Coshocton Co.: among mosses at base of *Fagus grandifolia* tree above ravine, N. A. E. W., *King 921a*, det. Nearing; associated with *Cladonia coniocraea*, *Parmelia rudecta*, and *Physcia sorediata*, N. A. E. W., *King 1059*, in part, det. Nearing.

Physcia sorediata (Ach.) Nearing—Coshocton Co.: associated with *P. endochrysea*, *Parmelia rudecta*, and *Cladonia coniocraea*, N. A. E. W., *King 1059*, in part, det. Nearing.

Physcia tribacia (Ach.) Nyl.—Coshocton Co.: among mosses at base of *Fagus grandifolia* tree above ravine, N. A. E. W., *King 921*, det. Nearing; associated with *Parmelia saxatilis* near Station, N. A. E. W., *King 948a*, det. Nearing.

Physcia sp.—Coshocton Co.: on bark of exposed roots of *Fagus grandifolia* tree above ravine, N. A. E. W., *King 905a*, det. with a question by Nearing.

LEPRARIACEAE

Amphiloma lanuginosum (Hoffm.) Nyl.—Coshocton Co.: at base of *Fagus grandifolia* tree above ravine, N. A. E. W., *King 922*, det. Nearing.

Crocynia zonata G. Anderson—Coshocton Co.: on sandstone rocks in woods about the bluffs in back of tower, N. A. E. W., *King 961*, det. Nearing; *King 964*, det. Nearing; *King 965*, det. Nearing.

REBOULIACEAE

Asterella tenella (L.) P. Beauv.—Coshocton Co.: on soil in pasture near Station, N. A. E. W., *King 1506*, det. Fulford.

JUNGERMANNIACEAE

Blasia pusilla L.—Coshocton Co.: on moist soil near Station, N. A. E. W., *King 944*, det. Wareham.

Cephaloziella hampeana (Nees.) Schiffn.—Coshocton Co.: associated with *Jamesoniella autumnalis*, N. A. E. W., *King 1491*, in part, det. Fulford, who says "either *C. hampeana* or *C. starkii* (Funck) Schiffn."

Frullania eboracensis Gottsche—Coshocton Co.: near Station, N. A. E. W., *King 1070*, det. Wareham; *King 1072*, det. Wareham.

Frullania sp.—Coshocton Co.: associated with *Ptilidium pulcherrimum*, N. A. E. W., *King 1490*, in part. det. Fulford.

Geocalyx graveolens (Schrad.) Nees—Coshocton Co.: associated with *Radula complanata* among mosses at base of *Fagus grandifolia* tree in woods near Station, N. A. E. W., *King 920*, in part, det. Wareham.

Jamesoniella autumnalis (P. DC.) Steph.—Coshocton Co.: on sandstone rocks in woods, N. A. E. W., *King 938*, det. Wareham; associated with *Cephaloziella* and forming a mat about 5 mm. thick on large boulders at side of ravine, N. A. E. W., *King 1491*, in part, det. Fulford.

Lophocolea heterophylla (Schrad.) Dumort.—Coshocton Co.: on moist clay, tree bark, and rotten wood, Lower Spoon Creek, N. A. E. W., *King 1466*, det. Fulford; *King 1467*, det. Fulford; *King 1470a*, det. Fulford; associated with *Entodon seductrix* var. *minor* on tree bark, Lower Spoon Creek, N. A. E. W., *King 1471*, det. Fulford; among lichens and mosses on soil of road bank, N. A. E. W., *King 1481*, det. Fulford; on soil and on base of *Fagus grandifolia* tree on bank, N. A. E. W., *King 1486*, det. Fulford.

Ptilidium pulcherrimum (Web.) Hampe—Coshocton Co.: associated with *Frullania* in colony about 2.5 cm. square on large boulder at side of ravine, N. A. E. W., *King 1490*, in part, det. Fulford.

Radula complanata (L.) Dumort.—Coshocton Co.: associated with *Geocalyx graveolens* among mosses at base of *Fagus grandifolia* tree in woods near Station, N. A. E. W., *King 920*, in part, det. Wareham; on rotten wood near Butternut Falls, N. A. E. W., *King 1507*, det. Fulford.

Riccardia pinguis (L.) S. F. Gray—Coshocton Co.: associated with *Physcomitrium turbinatum*, N. A. E. W., *King 1038*, in part, det. Wareham.

PORELLACEAE

Porella platyphylloidea (Schwein.) Lindb.—Coshocton Co.: associated with *Anomodon attenuatus* on sandstone rocks in woods near Butternut Falls, N. A. E. W., *King 1472*, det. Fulford.

METZGERIACEAE

Fossombronia sp.—Coshocton Co.: on soil in pastures, N. A. E. W., *King 1505*, det. Fulford.

Pellia sp.—Coshocton Co.: on moist soil in swamp above Butternut Falls, N. A. E. W., *King 1508*, det. Fulford.

DITRICHACEAE

Ceratodon purpureus (L.) Brid.—Coshocton Co.: on sandstone rocks in open fields, N. A. E. W., *King 913*, det. Wareham;[2] on soil in valley behind field warehouse, watershed 196, N. A. E. W., *King 927*, det. Wareham;[2] *King 928*, det. Wareham;[2] on soil in grass along roadside, N. A. E. W., *King 1084*, det. Wareham.[2]

Ditrichum pallidum (Schreb.) Hampe—Coshocton Co.: along roadsides, N. A. E. W., *King 982*, det. by Wareham as "*D. pallidum* (Hedw.) Hampe."

DICRANACEAE

Dicranella heteromalla (L.) Schimp.—Coshocton Co.: near Station, N. A. E. W., *King 945*, det. by Wareham as "*D. heteromalla* (Hedw.) Schimp."

Dicranella heteromalla var. *orthocarpa* (Hedw.) E. G. Britton—Coshocton Co.: on upper side of sandstone rocks in watercourse in ravine, N. A. E. W., *King 1494*, det. by Grout as "var. *orthocarpa* (Hedw.) Paris."

Dicranella rufescens (J. E. Sm.) Schimp.—Coshocton Co.: near Station, N. A. E. W., *King 977*, det. Wareham.

Dicranella sp.—Coshocton Co.: on floor of wooden bridge on tower road, N. A. E. W., *King 970*, det. Wareham.

Dicranum fulvum Hook.—Coshocton Co.: on large sandstone rocks in woods, N. A. E. W., *King 909*, det. Wareham; forming with soil a mat about 5 mm. thick on sandstone rocks in ravine, N. A. E. W., *King 1492*, det. Grout.

Dicranum montanum Hedw.—Coshocton Co.: near Station, N. A. E. W., *King 935*, det Wareham; on soil and on bark in fork of root-buttresses of *Fagus grandifolia* tree in woods near Station, N. A. E. W., *King 967*, det. Wareham; on base of *Fagus grandifolia* tree, N. A. E. W., *King 1085*, det. Wareham; along Lower Spoon Creek, N. A. E. W., *King 1469*, det. Grout.

Dicranum scoparium (L.) Hedw.—Coshocton Co.: near Station, N. A. E. W., *King 936*, det. by Wareham as "*D. scoparium* Hedw."

Dicranum viride (Sull. & Lesq.) Lindb.—Coshocton Co.: on bark of *Fagus grandifolia* in woods near field warehouse, N. A. E. W., *King 1489*, det. Grout.

Dicranum sp.—Coshocton Co.: on sandstone rocks, N. A. E. W., *King 937*, det. Wareham..

Oncophorus polycarpus var. *strumiferus* (De Not.) Grout—Coshocton Co.: near Station, N. A. E. W., *King 1501*, det. Grout

POTTIACEAE

Weisia viridula (L.) Hedw.—Coshocton Co.: on loose soil of roadside bank back of tower, N. A. E. W., *King 1077*, det. by Wareham as "*W. viridula* Hedw."

GRIMMIACEAE

Grimmia alpicola Hedw.—Coshocton Co.: near Station, N. A. E. W., *King 1485*, det. Grout.

FUNARIACEAE

Funaria flavicans Michx.—Coshocton Co.: growing among cinders in driveway to abandoned house on tower road, N. A. E. W., *King 974*, det. Wareham.

Physcomitrium turbinatum (Michx.) Brid.—Coshocton Co.: associated with *Riccardia pinguis*, N. A. E. W., *King 1038*, in part, det. Wareham.

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2 As "C. *purpureus* (Hedw.) Brid."

BRYACEAE

Bryum sp.—Coshocton Co.: forming mat on rocks at Butternut Falls, N. A. E. W., *King 1357c*, det. Grout.

Pohlia nutans (Schreb.) Lindb.—Coshocton Co.: associated with *Cladonia* on soil at base of tree on roadside bank in back of tower, N. A. E. W., *King 1076*, det. by Wareham as "*P. nutans* (Hedw.) Lindb."

Pohlia wahlenbergii (Web. & Mohr) A. L. Andr.—Coshocton Co.: in very wet soil of marsh on tower road, N. A. E. W., *King 1073*, det. Wareham.

MNIACEAE

Mnium cuspidatum (L.) Leyss.—Coshocton Co.: on rock edge, Butternut Falls, N. A. E. W., *King 1036*, det. Wareham;[3] on surface of dead logs and near ground in marsh back of tower, N. A. E. W., *King 1066*, det. Wareham.[3]

LESKEACEAE

Haplohymenium triste (Cesati) Kindb.—Coshocton Co.: at base of *Fagus grandifolia* tree in woods near Station, N. A. E. W., *King 918*, det. Wareham.

Leskea gracilescens Hedw.—Coshocton Co.: on stones by roadside ditches, N. A. E. W., *King 1482*, det. Grout.

THUIDIACEAE

Anomodon attenuatus (Schreb.) Hüben.—Coshocton Co.: associated with *Platygyrium repens* on bark of log in tower road region, N. A. E. W., *King 1083*, in part, det. by Wareham as "*A. attenuatus* (Hedw.) Hüben."; forming thick mats on sandstone rocks in woods near Butternut Falls, N. A. E. W., *King 1345*, det. Grout; *King 1347*, det. Grout.

Thuidium delicatulum (L.) Mitt.—Coshocton Co.: associated with *Sematophyllum*, N. A. E. W., *King 1060*, in part, det. by Wareham as "*T. delicatulum* (Hedw.) Mitt."

AMBLYSTEGIACEAE

Amblystegium serpens (L.) B. S. G.—Coshocton Co.: associated with *Hygroamblystegium irriguum* and *Chamberlainia acuminata*, forming thick mat-like growth on fallen log in marsh below tower road, N. A. E. W., *King 1066*, in part, det. by Wareham as "*A. serpens* (Hedw.) Bry. Eur., attenuated form"; forming mats on rocks at Butternut Falls, N. A. E. W., *King 1357a*, det. Grout.

Amblystegium varium (Hedw.) Lindb.—Coshocton Co.: near Station, N. A. E. W., *King 1082*, det. Wareham; *King 1479*, det. Grout; in soil mat on rocks at Butternut Falls, N. A. E. W., *King 1474*, det. Grout.

Campylium chrysophyllum (Brid.) Bryhn.—Coshocton Co.: forming soil layer on rocks at Butternut Falls, N. A. E. W., *King 1357*, det. Grout.

Hygroamblystegium fluviatile (Sw.) Loeske—Coshocton Co.: near Station, N. A. E. W., *King 1034*, det. Wareham;[4] on sandstone rocks by brook back of Station, N. A. E. W., *King 1483*, det. Grout.[4]

Hygroamblystegium irriguum (Hook. & Wils.) Loeske—Coshocton Co.: associated with *Amblystegium serpens* and *Chamberlainia acuminata*, forming a thick mat-like growth on fallen log in marsh below tower road, N. A. E. W., *King 1066*, in part, det. by Wareham as "*H. irriguum* (Wils.) Loeske"; forming thick mats on damp rocks at Butternut Falls, N. A. E. W., *King 1348*, det. Grout.

Hygroamblystegium orthocladon (P. Beauv.) Grout—Coshocton Co.: overgrowing the lichen *Leptogium tremelloides* near Station, N. A. E. W., *King 983*, det. Wareham; *King 1033*, det. Wareham.

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3 As "*M. cuspidatum* Hedw."
4 As "*H. fluviatile* (Hedw.) Loeske."

HYPNACEAE

Chamberlainia acuminata (Hedw.) Grout—Coshocton Co.: associated with *Amblystegium serpens* and *Hygroamblystegium irriguum*, forming a thick mat-like growth on fallen log in marsh below tower road, N. A. E. W., *King 1066*, in part, det. Wareham.

Homomallium adnatum (Hedw.) Broth—Coshocton Co.: near Station, N. A. E. W., *King 1353*, det. Grout, *King 1500*, det. Grout.

Hypnum curvifolium (Hedw.) Mitt.—Coshocton Co.: very abundant on sandstone rocks on wooded hillsides back of tower, N. A. E. W., *King 1054*, det. Wareham; associated with *H. molluscum* in woods near tower road, N. A. E. W., *King 1068*, in part, det. Wareham; in ravine near field warehouse, N. A. E. W., *King 1443*, det. Wareham.

Hypnum imponens Hedw.—Coshocton Co.: on sandstone rocks, N. A. E. W., *King 908*, det. Wareham; associated with *H. molluscum* in woods on tower road, N. A. E. W., *King 1080*, in part, det. Wareham.

Hypnum molluscum Hedw.—Coshocton Co.: associated with *H. curvifolium* and *H. imponens* in woods on tower road, N. A. E. W., *King 1068*, in part, det. Wareham; *King 1080*, in part, det. Wareham.

Hypnum patientiae Lindb.—Coshocton Co.: near Station, N. A. E. W., *King 1056*, det. Wareham; on moist soil in pastures above Butternut Falls, N. A. E. W., *King 1363*, det. Grout.

Leptodictyum trichopodium (Schultz) Warnst.—Coshocton Co.: associated with *Brachythecium acutum* on wet soil in marsh along tower road, N. A. E. W., *King 1074*, in part, det. Wareham.

Leptodictyum trichopodium var. *kochii* (B.S.G.) Broth—Coshocton Co.: near Station, N. A. E. W., *King 1477*, det. Grout; *King 1483*, det. Grout.

SEMATOPHYLLACEAE

Sematophyllum adnatum (Michx.) E. G. Britton—Coshocton Co.: on dead wood, N. A. E. W., *King 914*, det. Wareham.

Sematophyllum carolinianum var. *admixtum* (Sull.) Grout—Coshocton Co.: on large fallen sandstone rocks in ravine, N. A. E. W., *King 1493*, det. Grout; *King 1495*, det. Grout; *King 1502*, det Grout; *King 1503*, det. Grout.

Sematophyllum sp.—Coshocton Co.: associated with *Thuidium delicatulum*, N. A. E. W., *King 1060*, in part, det. Wareham.

BRACHYTHECIACEAE

Brachythecium acutum (Mitt.) Sull.—Coshocton Co.: associated with *Leptodictyum trichopodium* on wet soil in marsh along tower road, N. A. E. W., *King 1074*, in part, det. Wareham.

Brachythecium flagellare (Hedw.) Jennings—Coshocton Co.: on stones by woodland brook near Station, N. A. E. W., *King 910*, det. Wareham; near Station, N. A. E. W., *King 1032*, det. Wareham; on large rocks at Butternut Falls, N. A. E. W., *King 1355*, det. Grout; *King 1357b*, det. Grout; on sandstone rocks in ravine, N. A. E. W., *King 1497*, det. Grout; *King 1504*, det. Grout; on large sandstone rocks in watercourse in ravine near field wharehouse, N. A. E. W., *King 1499*, det. Grout; on soil near Station and on tower road, N. A. E. W., *King 1078*, det. Wareham; *King 1081*, det. Wareham.

Brachythecium flagellare var. *homomallum* (B.S.G.) Jennings—Coshocton Co.: on fallen rocks at Butternut Falls, N. A. E. W., *King 1360*, det. Grout; forming mats on stones in watercourse in ravine near field warehouse, N. A. E. W., *King 1498*, det. Grout.

Brachythecium rutabulum (Hedw.) B.S.G.—Coshocton Co.: on loose soil along roadside behind tower, N. A. E. W., *King 1067*, det. by Wareham as "*B. rutabulum* (Hedw.) Bry. Eur."

Brachythecium salebrosum (Hoffm.) B.S.G.—Coshocton Co.: associated with *Amblystegium varium*, N. A. E. W., *King 1480*, det. Grout.

Bryhnia graminicolor (Brid.) Grout—Coshocton Co.: on loose soil in low shady damp ground by a brook in back of tower, N. A. E. W., *King 1075*, det. Wareham.

Cirriphyllum boscii (Schwaegr.) Grout—Coshocton Co.: forming a dense mat over stones in woods by tower road, N. A. E. W., *King 1071*, det. Wareham.

Eurhynchium hians (Hedw.) J. & S.—Coshocton Co.: near Station, N. A. E. W., *King 1035*, det. Wareham.

ENTODONTACEAE

Entodon seductrix (Hedw.) C. Müll.—Coshocton Co.: near Station, N. A. E. W., *King 940*, det. Wareham.

Entodon seductrix var. *minor* (Aust.) Grout—Coshocton Co.: on tree bark, Lower Spoon Creek, N. A. E. W., *King 1470*, det. Grout.

Entodon sp.—Coshocton Co.: on bark of *Fagus grandifolia*, N. A. E. W., *King 1086*, det. Wareham.

Platygyrium repens (Brid.) B.S.G.—Coshocton Co.: in bark fissures and on exposed roots at base of *Fagus grandifolia* tree in woods near Station, N. A. E. W., *King 903b*, det. Wareham; [5] *King 905b*, det. Wareham; [5] *King 934*, det. Wareham; [5] *King 1087*, det. Wareham; [5] on logs in valley behind field warehouse, N. A. E. W., *King 924*, det. Wareham; [5] associated with *Anomodon attenuatus* on bark of log in tower road region, N. A. E. W., *King 1083*, in part, det. Wareham; [5] near Station, N. A. E. W., *King 1438*, det. Grout; associated with *Parmelia* 5-6 feet from ground on bark of *Wallia cinerea*, N. A. E. W., *King 1475*, det. Grout; on bark of *Fagus grandifolia*, N. A. E. W., *King 1478*, det. Grout.

HEDWIGIACEAE

Hedwigia ciliata Hedw.—Coshocton Co.: associated with lichens on sandstone rocks, N. A. E. W., *King 931*, det. Wareham; *King 933*, det. Wareham.

BRASSICACEAE

Armoracia lapathifolia Gilib.—Coshocton Co.: growing along roadside on east-west road past the strip mine, N. A. E. W., *King s.n.*

CORNACEAE

Cornus officinalis Sieb. & Zucc.—Lorraine Co.: in outdoor cultivation, coll. William Wright, Oberlin, *Moldenke 14921*, verif. Bailey.

LAMIACEAE

Teucrium canadense f. *albiflorum* House—Coshocton Co.: in moist overgrown field in company with *T. canadense* var. *virginicum* (L.) Eaton, N. A. E. W., *Moldenke 13005*, reported in my first contribution as var. *virginicum*.

Unidentified cryptogams—Coshocton Co.: *King 925*, *King 1063*, *King 1385*, *King 1399* (possibly some member of the *Eurotiaceae*), *King 1407*, *King 1408*, *King 1409*, *King 1410*, *King 1411*, *King 1413*, *King 1414*, *King 1415*, *King 1419*, *King 1420*, *King 1423*, *King 1427*, *King 1434*, *King 1436*, *King 1441*, *King 1468*.

Supplementary to footnote 14 in the first paper of this series [6] regarding the spellings of the specific epithet "*pensylvanica*" it may be noted that Michaux and Wangenheim each published a *Rosa pensylvanica*, Willdenow proposed *Struthiopteris pensylvanica*, and Fernald *Pteretis pensylvanica*, while H. C. Andrews published a *Rosa pennsylvanica*, Schwaegrichen proposed a *Grimmia pennsylvanica*, Gable an *Azalea pennslyvanica*, Ashe a *Crataegus pennsylvanica*, and Rehder a *Rhododendron pennsylvanicum*.

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5 As "*P. repens* (Brid.) Bry. Eur."

6 Castanea **9**:80. 1944.

Some Algae from Pope County, Illinois

Harry K. Phinney

An opportunity to collect algae in southern Illinois presented itself in the summer of 1944 when I was stationed at Lake Glendale in Pope County, as a member of the Illinois State Natural History Survey. Lake Glendale is an 80 acre artificial lake, located in the Robbsville Recreational Area of the Shawnee National Forest. The dam creating the lake was completed and the valve impounding the water closed in the fall of 1939. During the spring of 1940, Survey crews stocked the lake with fish and planted a number of species of aquatic and semi-aquatic plants about the margin. By 1944 Typha and Potamogeton had occupied all of the shallows to a depth of one and one-half meters, and *Chara sejuncta* A. Br. had colonized out to a depth of three meters. Collections of algae were made from open pools in the Typha beds, from entangled masses growing over the Potamogeton and Chara, from algal mats floating in open water, from growths on logs, stumps and mud in shallow water, from the stone and concrete work of the dam and spillways and from the sand and soil about the margin of the lake.

A few collections were also made from a number of stock ponds that have been constructed on the lands of the University of Illinois Agricultural Experiment Station which is located in Pope County in the neighborhood of Lake Glendale. Collections from this source are not numerous as rapid sedimentation has rendered the edges of most of these ponds unapproachable. The Typha beds are very dense and have encroached to the inner limits of deep water and have thus reduced the favorable algal habitats.

I would like to express my appreciation to Drs. T. H. Frison and G. W. Bennett of the Illinois Natural History Survey for their decision appointing me temporarily Assistant Aquatic Biologist for the summer of 1944. I am particularly grateful to Dr. D. F. Hansen who is in immediate charge of the Survey's Lake Glendale project, for his encouragement and help in the work which made possible these collections. The assistance of R. Webb of the Southern Illinois Agricultural Experiment Station in making the ponds on University property accessible is hereby acknowledged.

The identification of the Myxophyceae was done by Dr. F. Drouet of the Chicago Natural History Museum and of the Characeae by F. K. Daily of the Herbarium of Butler University. The identification of the remaining specimens and the preparation of the manuscript was carried out in the botanical laboratories of Yale University with the aid of the Theresa Seessel Fellowship.

Specimens of all of the collections listed have been deposited in Herbarium of the Illinois Natural History Survey, in the Cryptogamic Herbarium of the Chicago Natural History Museum and in my personal herbarium. Collections listed without specific locality data were taken from Lake Glendale. The arrangement of the genera follows the order of Smith's *Fresh-Water Algae of the United States.*

CHROOCOCCACEAE

Chroococcus rufescens (Kütz.) Näg., in seepage on the spillway of the dam, 14 July, *973*.

Aphanocapsa Richteriana Hieron., over submerged vegetation, 1 Sept., *1067*.

OSCILLATORIACEAE

Oscillatoria Agardhii Gom., over submerged vegetation, 16 Aug. *1028;* large floating masses along the north shore, 31 July, *990;* washed into the sand of the beach, 19 July, *987;* large floating masses in Wells' Pond, 5 July, *969*.

O. princeps Gom., floating in the shallows along the north shore, 15 July, *984;* on mud in the shallows of the south shore, 15 July, *980*.

O. tenuis Gom., small floating masses along the south shore, 1 Sept., *1067;* floating in cove by large shelter house, 1 Aug., *1031*.

Phormidium Retzii Gom., on moist rocks in woodland creek at the head of the lake, 1 Aug., *922*.

P. uncinatum Gom., in drainage from the fill of the dam, 14 July, *971*.

Porphyrosiphon Notarisii Gom., on bare soil in gully in old field north of the lake, 12 July, *970*.

Microcoleus rupicola (Tild.) Dr., with *Fischerella ambigua* (B. & F.) Gom., on sand bathing beach 9 June, *922;* on clay-sand above the bathing beach, 9 June, *920;* on earth-fill of dam, 14 July, *974;* on soil at margin of Jennings' Pond, 26 Aug., *1039*.

M. vaginatus Gom., with *Schizothrix purpurascens* Gom., on soil among tall weeds at the south end of the dam, 12 Aug., *1017 & 1025;* with *Scytonema ocellatum* B. & F., on a clay bank at the dam, South Pasture Pond, 28 Aug., *1050*.

Microcoleus sp., on the sand of the bathing beach, 10 June, *913*.

Schizothrix purpurascens Gom., on dry earth-fill of the dam, 14 July, *978;* with *Microcoleus vaginatus* Gom., on soil among tall weeds at the south end of the dam, 12 Aug., *1017 & 1025;* on soil of a grassy bank on the south shore, 10 June, *946*.

S. Stricklandii Dr., with *Microcoleus rupicola* (Tild.) Dr., on sand among sedges on the bathing beach, 9 June, *926*.

S. lacustris Gom., on rocks in valve channel below the dam, 12 Aug., *1020*.

NOSTOCACEAE

Anabaena unispora Gardn., as a thin gelatinous floating film among the pondweeds, 16 Aug., *1027;* over Chara in the shallows, 15 July, *982*.

Cylindrospermum muscicola B. & F., on damp soil along the spillway, 14 July, *976*.

SCYTONEMATACEAE

Scytonema ocellatum B. & F., with *Microcoleus vaginatus* Gom., on a clay bank at the dam, South Pasture Pond, 28 Aug., *1050*.

Plectonema Nostocorum Gom., with *Fischerella ambigua* (B. & F.) Gom., and *Microcoleus* sp., in the sand of the bathing beach, 10 June, *924;* on rocks along the valve spillway, 12 Aug., *1032;* on clay soil at the margin of Jennings' Pond, 26 Aug., *1035*.

STIGONEMATACEAE

Fischerella ambigua (B. & F.) Gom., with *Scytonema ocellatum* B. & F., in the sand of the bathing beach, 9 June, *925;* on rocks in the valve spillway, 12 Aug., *1019*.

RIVULARIACEAE

Amphitrix janthina B. & F., with *Calothrix parietina* B. & F., on the concrete floor of the shower in the bath house, 6 Aug., *1013;* in the bowl of an outdoor drinking fountain at the bath house, 6 Aug., *1015*.

Calothrix parietina B. & F., with *Schizothrix lacustris* Gom., on the wall of a scale-pit on the University farm, Lake Glendale, 14 July, *977*.

BOTRYDIACEAE

Botrydium granulatum (L.) Grev. on clay soil at the margin of Wells' Pond, 26 Aug., *1045*.

PALMELLACEAE

Gloeocystis confluens (Kütz.) Richt., on a clay bank on the south shore, 10 June, *949;* on wood in exposed bottom sediments at the head of the lake, 4 Aug., *1009;* on soil at the margin of Jennings' Pond, 26 Aug., *1039.*

ULOTRICHACEAE

Stichococcus flaccidus (Kütz.) Gay, on soil among the grass above the sand beach, 9 June, *921.*

S. subtilis (Kütz.) Klerck., on a clay bank along the south shore, 10 June, *949;* on dry soil of a gully near the dam, 5 June, *913.*

CLADOPHORACEAE

Basicladia Chelonum (Coll.) Hoffm. & Tild., on the shell of a snapping turtle from Lake Glendale, 25 July, *989.*

OEDOGONIACEAE

Oedogonium Borisianum (LeCl.) Wittr., with *O. mitratum* Hirn, on a charred stump at the head of the lake, 26 July, *954.*

O. Landsboroughi (Hass.) Wittr., on roots in the water along the south shore, 26 June, *968.*

O. mitratum Hirn, over Chara in shallow water, South Pasture Pond, 28 Aug., *1052 & 1054.*

O. Reinschii Roy, sterile, sparingly mixed with sterile *Oedogonium* sp. over submerged aquatics, 1 Aug., *933.*

Bulbochaete intermedia var. *depressa* Wittr., with *B. pygmea* Pringsh., on submerged dead Typha, 26 June, *953.*

B. pygmea Pringsh., on submerged dead Typha, 26 June, *952.*

PROTOSIPHONACEAE

Protosiphon botryoides (Kütz.) Klebs, on soil at the margin of Jennings' Pond, 26 Aug., *1039.*

ZYGNEMATACEAE

Zygogonium ericetorum Kütz., on soil at the south end of the dam, 12 Aug., *1018.*

Spirogyra nitida (Dillw.) Link, over submerged aquatics in shallows, 26 June, *955, 958 & 959.*

S. setiformis (Roth) Kütz., deeply submerged, 26 June, *965;* floating in valve spillway, 12 Aug., *1022;* over submerged vegetation at the head of the lake, 1 Aug., *994;* over vegetation in shallow water, South Pasture Pond, 28 Aug., *1047.*

DESMIDIACEAE

Pleurotaenium truncatum (Breb.) Näg., floating along the north shore, 26 June, *962.*

Cosmarium circulare Reinsch, drift along the shore, 5 & 9 June, *911, 914 & 927.*

Micrasterias apiculata (Ehr.) Menegh., over vegetation in the shallows, 26 June, *961.*

Onychonema filiforme (Ehr.) Roy & Bliss., over submerged vegetation, 1 Sept., *1062.*

Hyalotheca mucosa (Dillw.) Ehr., on vegetation and roots in very shallow water, 10 June, *947 & 948.*

CHARACEAE

Chara sejuncta A. Br., from Lake Glendale, 26 June *967;* same, 18 Aug., *1032;* from Jennings' Pond, 26 Aug., *1034 & 1042;* from South Pasture Pond, 28 Aug., *1049;* from Hooker Pond, 28 Aug., *1056 & 1059.*

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Notes and Discussion

Changes in Botanical Names

C. A. Weatherby

In 1755 John Hill wrote a pungent preface to his Family Herbal. In it he accused botanists of wasting their time on trivia to the neglect of practical considerations. He asserted that more new and strange words had been introduced into botany "than into all the Sciences together" and that Linnaeus had been so guilty in this particular line of misdemeanor that a good scholar would not "be able to understand three lines together in his best Writings." He declared that he was going to write a book in which each plant would be called by one name only in English and one in Latin and those the most familiar, "no matter what Caspar, or John Bauhine, or Linnaeus call them."

Anyone who has read certain journals during the past year will at once detect something familiar here. It is an old complaint, often enough repeated, that botanical nomenclature ought to be fixed and isn't. Lately it has been given particularly articulate utterance by three writers: Dr. W. M. Harlow, Journ. Forestry **43**:403-406; Mr. A. C. Martin, Am. Midl. Nat. **34**:799-800; and Prof Earl L. Core, Castanea **10**:116-119. The taxonomist, mindful of the relative esteem in which the work of Linnaeus and that of Hill is now held and struggling to understand and to keep in order his methods of dealing with a world of plants which refuses to be orderly or logical, may be pardoned if he grows as irritated at these repetitions as the complainants are impatient with his slow progress, and grumbles to himself that he knows his business and it is none of theirs. So long as he is merely called a name-tinker and told that his chief motive is to get his name into an author-citation, he can, indeed, ignore it. But the present protests deserve more respectful treatment; they touch on one real evil and they make some attempt to suggest remedies—even though these are, unanimously, calls upon somebody else to do something. Dr. Harlow's remedy is a flat, if temporary, defiance of the rules of botanical nomenclature by the United States Forest Service; Mr. Martin's is a "well financed" (he does not say how) national commission to prepare a permanent check-list of names of species occurring in the United States; Prof. Core's is new legislation, the exact nature of which he does not specify, by the next botanical congress. Mr. Martin, at least (and I think the others would agree) recognizes that changes must occur because of advances in knowledge and of differences as to what still remains a matter of taxonomic opinion, the limits of genera and species. Such changes they would presumably accept, albeit with some reluctance! I hope they would add correction of past errors. But, with all these saving graces, none of the three authors makes the thorough analysis of the case which one would suppose a prerequisite to effective remedy; and none of them seems to be aware of the remedial agencies which already exist.

Most purely nomenclatural changes of name come about in one of three ways: (1) because of the discovery of an earlier, different name for the same species; (2) because the same name has been earlier used for a different species (homonym rule); (3) through the application of the type method.

(1) and (2) are results of the rules as to priority and may be considered together. Under them, the original name disappears and is replaced by a different one.[1] The principle of absolute priority in specific epithets was adopted by taxonomists in the full knowledge that it would cause temporary upsets and inconvenience, especially in England and America where the "Kew rule" of the first name under the genus had been in use for a considerable time. But it appeared to be, and still appears to be, the only

[1] That particularly sore spot, *Sequoia gigantea*, belongs here. So d es *Abies nobilis*, mentioned by Dr. Harlow.

means of achieving the end of one name for one species in a perfectly clear-cut and indisputable way. It has been in the rules only since 1905—to the taxonomist, conscious that science, as well as art, is long, a relatively little while. That we are no nearer bedrock than we are (and we may be much nearer than our impatient friends suppose) is because there are a very great number of species in the world and a still larger number of names for them, and only a few taxonomists, not immune from mistakes. Conservation of specific names, as a general principle, was rejected by the congresses of 1930 and 1935 for a variety of reasons, all to be summed up in the one word impracticability.

The latter congress, however, authorized a limited form of specific conservation. It appointed an international committee, headed by the English forester, Burtt Davy, to draw up a list of names of economic plants according to the International Rules, this list to stand unaltered for ten years, no matter what happened meantime. This is less than Mr. Martin desires; but it is a definite step toward stabilization. The committee began its work; how far it had proceeded when it was interrupted by the war, I do not know. Burtt Davy has died, but the secretary of the committee, Miss M. L. Green (now Mrs. T. A. Sprague) happily survives, with an enviable and deserved reputation for efficiency. If Mr. Martin wishes to do something concrete and immediate for stabilization, he should, instead of attempting to set up another committee, draw up a list of species whose names he thinks should be fixed, with some statement of his reasons, and send it to Miss Green, Royal Botanic Gardens, Kew, Surrey, England. Dr. Harlow might add his list.

In the third sort of change, that due to typification, the original name remains, but is shifted to another species.[2] In considering such cases, it should be borne in mind that the "type method" of fixing the application of specific epithets by attaching them irrevocably to a representative specimen, illustration or description is something relatively new, which did not appear in the rules until 1930 and is not yet fully assimilated by some of the Europeans (witness the debate at Amsterdam on Art. 54 of the rules, Proc. 6th Int. Congress 1: 347 ff.). It has to be superimposed on the work of early authors who never even imagined it. The Congress of 1930, realizing the difficulty of this process and not favorably impressed with the results in action of the rather elaborate provisions for choosing types in the 1905 edition of the American Code, wisely deferred the setting up of any regulations, leaving the choice of types to monographers and others who had to deal with it and were presumably best qualified to do so.

Inconveniences and uncertainties in matters of typification are, then, to be regarded as growing pains incident to the working out, in practice, of a usable system. It can now be seen that most of our real troubles, except those due to plain misidentification of types, have arisen from typifications made on technical and theoretical grounds, without regard to usage. In this connection, Dr. Svenson has rendered valuable service by pointing out, in his noteworthy article on the descriptive method of Linnaeus (Rhodora **47**:297-302, 363-370), that composite Linnaean species may be typified by any included element without doing violence to any concept of their author. If, then, Prof. Core wishes to do something definite, the time is ripe for him to propose an addition to the rules providing: (1) that in choosing lectotypes for Linnaean and other early species, the preservation of well-established usage must be the primary consideration: (2) that where usage is not a clear guide, typification by a previous author is to be accepted if in consonance with the rules and not demonstrably in error. Such a rule would restore *Quercus rubra* to its old place and would largely prevent such arguments as have arisen over the application of the name *Caesalpinia Crista* (Journ. Bot. **76**: 175 ff., 1938).

No committee and no congress can of itself cover its whole field; it must have detailed proposals from those immediately concerned on which to work.

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2 *Quercus rubra*, another cause célèbre, and *Juncus tenuis*, cited by Prof. Core, are in this category.

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Stolons of Carex assiniboiensis Boott in Iowa

W. L. Tolstead

While collecting 2½ miles northwest of Decorah, Winneshiek Co., Iowa, near the only known locality for *Chrysosplenium iowense* Rydb., *Carex assiniboiensis* Boott was found with culms 1 - 1½ mm. wide elongated into stolons 7 to 10 dm. in length and with small leaves and roots formed at the ends. The stolons had 5 to 8 nodes with sheaths 2 - 6 cm. and blades 3 - 12 cm. in length. Mackenzie's monograph of Carex does not record the presence of stolons and Dr. F. J. Hermann states in a letter of Sept. 3, 1943, that he has never seen this kind of growth in *C. assiniboiensis*. In one specimen, however, in the Missouri Botanical Garden (L. S. Cheney 4519) found near Mason, Bayfield Co., Wisconsin, July 6, 1896, a single culm shows a slightly abnormal elongation. In this specimen as well as in the one (Tolstead 7749) collected in Iowa on June 18, 1942, the seeds are matured fully. In the latter collection none of the fruiting culms bore more than 3 seeds and some were completely sterile.

Specimens collected in the same area (W. L. Tolstead 345) June 2, 1934, showed no growth of stolons and fruits were abundant. At that time the plants grew beneath a dense canopy of elm, linden and maple trees. During 1940 or 1941, however, the canopy of deciduous trees was opened considerably by cutting to make way for road-building 5 to 10 yards below the spot where the Carex plants were growing. For this reason the plants with stolons had been subjected to more than usual sunlight for at least one entire growing season and also during the spring of 1942. This suggests that development of stolons may be a reaction to increased light.

Further observations are desirable on the vegetative habits of this species especially after maturation of seed. This should indicate whether stolons are normally produced in summer after the flowering period is over. Herbaria are lacking plants of Carex in this stage of development because specimens are seldom collected after the seed matures.

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Polygonum Douglasii Greene not in Iowa

Henry S. Conard

In two papers on the flora of Winneshiek County, Iowa, Shimek listed *Polygonum Douglasii* as occurring with *Potentilla tridentata* on a knob of St. Peter Sandstone near Hesper. The specimens which he collected on several occasions prove to be *Polygonella articulata* (L.) Meisn., which is known also from Allamakee, Hardin and Clinton Counties, "very rare."

DEPARTMENT OF BOTANY,
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Book Reviews

BRAZIL. ORCHID OF THE TROPICS. By M. B. and R. S. Foster. In Dulau's Catalogue 295, recently issued, this book is described as follows: "Brazil—Adventurous excursions to bring back alive Bromeliads, air-minded Orchids, and Cacti." Jaques Cattell Press, Lancaster, Pennsylvania, 1945. 314 pp., maps and illustrations, 8vo. $3.50.

This is a readable and entertaining account of two visits to southeastern Brazil by a pair of enthusiastic collectors. Successful beyond expectations in the inquest of specimens, the authors also gathered, as they traveled about, an array of amusing and sometimes naive impressions of life and conditions in parts of Brazil. The account of a hasty visit to a Polish colony in Espirito Santo will be of special interest to those who have read Graça Aranha's "Canaan."

The book is amply illustrated with photographs and drawings by one of the authors. What is impressive about the account is the immense number of bromeliads collected, thanks, not only to the abundance encountered of these mostly not very accessible plants, but equally to the authors' untiring energy and concentration on their specialized task.

In a notice of a book with so flamboyant a title it may seem ungracious to be critical of botanical details, but since a copy was sent to this journal for review, various botanical mistakes might well be pointed out. The "royal" palms of the Rio botanical garden, or "imperial palms" as Brazilians often prefer to call them, are not the "royals" of Florida and Cuba, *Roystonea regia*, but the "cabbage" palms of Barbados and Venezuela, *R. oleracea*. The old Piassaba palm in the same garden has appeared to be almost on the point of death for the last twenty years, and presumably longer, but *funifera* does not mean "sad" or "funereal." The Brazil wood or Pernambuco wood, "pau brasil," *Cæsalpinia ecchinata*, is not "brasilette" or "brasiletto" which is *Haematoxylon campechianum* of the West Indies and Central America.

The Copernicia palms that the authors saw in abundance on their way to Corumba, or thereabouts, are *C. australis*, the Carandá, not the Carnaúba, *C. cerifera*, which belongs one to two thousand miles away in the semi-arid northeast of Brazil. The Brazilian eulogy of the latter which the authors quote does not apply to the former.

As to "a pigpen of solid mahogany" with orchids in São Paulo, this may be literally true as to the orchids, but if any mahogany exists in São Paulo it is likely to be in the form of some much prized piece of furniture brought from France where mahogany from Santo Domingo or from Africa is known as "acajou." Though mahogany exists in the far away Amazon region and is exported from above Manaos under the Spanish name "caóba," all of the wood goes to England or the United States. Its identity with mahogany or acajou, Portuguese "mogno," appeared not to be known a few years ago even to the collectors of export revenue. If a board of it under any name should reach São Paulo after 3500 miles of transportation by sea, it would be quite as valuable there as in Florida.

Samples of minor details more or less off color are: "gorgeous Raffia seeds"; "adobe" applied to the kind of rustic wall construction plastered with clay or mud that the Brazilians call "taipa"; "farofa" for farinha; "mate cha," "muito rocas" etc. The date of Cabral's landing in Brazil was 1503 and the place not the bay of Bahia.

Compared with the authors' real achievement such minor slips and errors are of course of little importance. Though they are, as publishers may some day discover, a regular feature of all quick and lively travelogues, they could be eliminated in editing and proof reading. The authors may be congratulated and assured of endless credit for their work of assembling so much special botanical material in the form of herbarium specimens and living plants.—B. E. DAHLGREN, Chicago Natural History Museum.

A MANUAL OF SOIL FUNGI. By Joseph C. Gilman. Iowa State College Press, Ames, Iowa. 1945. xi+392 pp., 135 figs. $5.00.

The exceedingly useful "Summary of the Soil Fungi" by Gilman and Abbott, published in 1927, has long been unobtainable and there has been nothing to take its place. It is a matter for gratification, therefore, that the senior author has very greatly enlarged the scope of that work and has brought it up to date in the form of the volume here noticed. As the author points out, it is difficult to state with precision what constitutes a soil fungus. He has restricted the treatment to those forms which have been reported as having been isolated from soils and which may be grown in culture in recognizable form. This excludes certain groups, notably the large terrestrial Basidiomycetes. It is not intended to suggest that these fungi are negligible in this relation, but the approach to their study and identification requires a different set of techniques. The author has drawn freely from special treatises on certain groups where such are available, notably in the case of *Aspergillus*, *Penicillium*, *Fusarium*, the Mucorales and the water molds. Nearly all genera are illustrated by line drawings showing characteristic structures. While simple, most of these are well chosen and decidedly helpful; some could be redrawn to advantage. A bibliography of 169 titles will guide the student who wishes to go more deeply into this field.

It is to be anticipated that this book will achieve wide usefulness. If revised at appropriate intervals it may well become the standard in this field.—G. W. MARTIN.

ORGANISME ET SEXUALITÉ. By M. Caullery. Encyclopédie Scientifique. G. Doin & Cie., Paris, 1942. 342 pp., 107 figs. Paperbound, $2.30.

With few exceptions all major groups of plants and animals reproduce sexually regardless of other forms of reproduction which may be characteristic of their respective life cycles. Thus the comprehensive title of the book may be justified in general terms. Accordingly, the author has included the better known representatives of both kingdoms ranging from Protista to flowering plants and mammals.

A short Introduction dealing with gametogenesis and syngamy is followed by four parts: Sex and Secondary Sex Characters, Sex Hormones, Sex Determination, and Differentiation of Sexes and Their Natural and Experimental Abnormalities, Intersexuality and Gynandromorphism. Appended are lists of selected references (arranged by chapters) and indices to authors' and specific names.

Written mainly from a zoological point of view, zoologists will certainly find it more useful than botanists. Fortunately our knowledge of sexuality, especially in plants, has progressed far beyond the status recorded in this book. Nevertheless, *Organisme et Sexualité* is the best brief introduction to the whole subject of sexuality available at the moment.—THEO. JUST.

FLORA OF OAKLAND COUNTY, MICHIGAN. A Study in Physiographic Plant Ecology. By Marjorie T. Bingham. Bulletin No. 22 of the Cranbrook Institute of Science, Bloomfield Hills, Michigan. 1945. 155 pp., illustrated.

Apparently based on extensive as well as intensive painstaking field work, this bulletin brings an interesting as well as scientifically valuable account of the plants and forest types of a single Michigan county. The study is introduced by a brief account of the geology of Michigan, and by a short review of historical records with reference to the vegetation as the pioneers found it.

Instability of scientific names no doubt justifies at present the use of Gray's Manual, 7th edition as the sole authority for names. It seems, however, that for the grasses Hitchcock's much more recent *Manual of the Grasses of the United States* could have been used. It might also be pointed out that some of the species listed for the county (now apparently extinct in the area) by earlier workers, who left no records in herbaria, were no doubt incorrect identifications. Mr. C. C. Deam (*Flora of Indiana*) found many such errors when checking herbarium specimens backing up such unusual records for Indiana.

The study is an excellent contribution to records of local flora. We have need of more of such field-centered studies. The numerous illustrations of habitats and vegetation types are clear as well as artistic and add their share to the value of the whole publication.—J. E. POTZGER, Butler University.

CATALOGUE OF ILLINOIS ALGAE. By Max E. Britton. Northwestern University Studies in the Biological Sciences and Medicine. No. 2, Evanston, Ill. 1944. Pp. viii + 177. $3.00.

Illinois has been the scene of considerable work in limnology, taxonomy, and pollution surveys and it is fitting that the accumulated studies be summarized in an orderly fashion for best evaluation of the whole. Britton's catalogue fills an important role in this respect, since it includes a review of the literature, a list of known species collections, references to nomenclature and the species distribution records within the state.

The systematic arrangement of the algal groups follows the scheme of G. M. Smith in his "Freshwater Algae of the United States." Within the families genera are listed in alphabetical order, as are the species under each genus. Only species records are reported. A sincere attempt has been made to include all the more pertinent data on the species records. Following each species name is a reference which is intended as a guide to a modern authority for the name and synonymy and to other recent information on the species. Collection data include the collector's name, the reference date (if any), the county name, and, commonly, additional details of habitat etc. The sources of information are clearly indicated in the bibliography at the back. The index to species, though not essential in a catalogue of this type, should add to convenience in use.

The catalogue lists 178 genera and 962 species, varieties and forms for Illinois, (including 279 species of diatoms). In comparison 1000 species and varieties have been reported for Iowa exclusive of the diatoms, and in Indiana over 660 species have been listed.

Many of the records appear in print for the first time, the additions having originated chiefly from the respective collections of Britton, F. Drouet, and E. N. Transeau. Nevertheless the list of algae in the catalogue will probably be considerably enlarged with future work. For example, in the Volvocales more than 60 genera of unicellular algae have been described, yet only 3—*Chloraster*, *Carteria*, and *Sphaerella*, represented by one species each—appear in the book as occurring in Illinois. The well-known type, *Chlamydomonas*—a genus of more than 300 species according to the latest monograph—apparently has never been identified in Illinois. The specialists in this group of motile unicells, many of which lack a cell-wall, have found it expedient to utilize characteristics of the living cells in their classification. This may at least partially explain the peculiar distributions indicated since most phycologists in this country—perhaps in the spirit of modern times—seem to prefer the hardier dehydrated specimens to the relative exclusion of Chlamydomonas and companion forms classified otherwise. Now that the deficiency is apparent perhaps the students of algae in the "Sucker State" will take an interest in the juicier varieties.

On the demerit side it should be mentioned that in the species distribution map of Illinois at the front of the book, the county names are illegible and the reader must provide himself with a map of his own for use as a key. The print throughout the book is unnecessarily large, on the whole, but the species names are set out at the margin for ease in use.

Britton is to be commended for doing a difficult task well. The catalogue should prove an important aid to later more extensive work not only as related to Illinois but also to the United States.—NOE HIGINBOTHAM.

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The

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